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Bulletin of the
British Museum (Natural History)

Observations on the systematics of the genus *Difflugia* in Britain (Rhizopoda, Protozoa)

Colin G. Ogden

Zoology series Vol 44 No 1 27 January 1983

The *Bulletin of the British Museum* (*Natural History*), instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

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Observations on the systematics of the genus *Difflugia* in Britain (Rhizopoda, Protozoa).

Colin G. Ogden

Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Synopsis

Detailed descriptions of the shell structure in thirty-eight species of *Difflugia* are given, and further information on one species which has been redescribed in an earlier report (Ogden & Fairman, 1979) is included. Two new species, *Difflugia hiraethogii* and *D. stoutii,* are described, and other systematic changes include the following new combinations: *D. cylindrus* (Thomas, 1953), *D. lacustris* (Penard, 1899), *D. microclaviformis* (Kourov, 1925), *D. microstoma* (Thomas, 1954), *D. parva* (Thomas, 1954), *D. tenuis* (Penard, 1890), *D. tricornis* (Jung, 1936), *D. venusta* (Penard, 1902) and *D. distenda* nom, nov., *D. gassowskii* nom, nov., *D. paulii* nom. nov., *D. rotunda* nom. nov. Seventeen of these redescriptions are new records for the British Isles. The structure of the shell is discussed and the patterning of the organic cement which binds the particles together is shown to be a useful taxonomic character.

Introduction

The taxonomy of specimens belonging to the genus *Difflugia* is based mainly on differences in size and shape of the agglutinated shells constructed by these animals. Comparison of cytoplasmic features are either difficult or impossible because most of it is encased by the shell which is often opaque. Differences in the shell features have resulted in about three hundred named species, varieties and forms being currently attributed to the genus. This proliferation of species is due to a combination of the lack of good diagnostic features and inadequate descriptions. The problem is clearly shown in the only comprehensive survey of the genus, based on African specimens, by Gauthier-Lièvre and Thomas (1958). In this work the authors had difficulties with several groups of individuals which shared common features, and as a result, about half of the 129 species described were designated as varieties or forms.

Some earlier studies (Ogden, 1979, 1980; Ogden & Fairman, 1979) were concerned with the variation of specimens having a pyriform shell, and the surface

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ultrastructure as revealed by the scanning electron microscope. The results showed that there was usually a limited variation in size, shape and composition of the shell within a species, whilst in some instances the patterning of the organic cement which binds the particles together was a reliable specific character. The present account uses the experience gained from these previous studies to extend the examination of shell structure in *Difflugia,* and to establish specific features for ten of the varieties of *Difflugia oblonga* listed by Gauthier-Lièvre and Thomas (1958). Thirty nine species are described, of which some are new records for the British Isles. Some 600 specimens have been examined and over 3000 micrographs representing different aspects of the shells are retained in the Protozoa Section, Department of Zoology as part of the study collection.

Materials and methods

Samples have been collected from several localities in England and Wales during the last four years. The material gathered varied from mosses, water plants including the substrate associated with the roots, and clumps of algae. Type of habitat ranged from areas of bog, banks of streams and small ponds in the New Forest, Lake District and North Wales to the dykes and rivers of Norfolk and Suffolk. Information relating to locality, date and type of sample is given with the description of each species as several have been found in more than one habitat.

Specimens of *Difflugia* were selected by searching through small isolates of material in a petri dish. Specimens were extracted using a glass micropipette, washed in several transfers through distilled water, and then individual shells were manipulated with a single-hair brush onto a small drop of Araldite on a previously cleaned cover slip. When about twenty specimens were positioned on each cover slip it was glued with Araldite onto a standard aluminium stub. In a few instances the very small delicate specimens collapsed before or during manipulation, this problem was overcome by transferring the washed specimens in a small drop of water onto cleaned cover slips and allowing it to dry. Prepared stubs were coated evenly with gold or gold/palladium, using a conventional sputter coating device, and examined in a Cambridge Stereoscan S180 operating at 10kV. The results were recorded on Ilford HP5 film.

Systematic descriptions

In a previous review (Gauthier-Lièvre & Thomas, 1958) of the genus the species were divided into ten groups, namely; lobed, collared, compressed, urceolate, globose, ovoid-globose, elongate, acute angled, horned and pyriform, but no particular significance was attached to these groupings. However, it does show the diversity of shell shape that has been included in the genus. Similarly in this report the species have been grouped together, the pyriform and elongate species are described first, followed by those which are pointed or have aboral protruberances, then the ovoid or spherical and finally the two compressed species.

Pyriform and elongate species

Difflugia bryophila (Penard, 1902) Jung, 1942

Difflugia pyriformis var. *bryophila* Penard, 1902
Difflugia oblonga var. *bryophila* (Penard, 1902) Gauthier-Lièvre & Thomas, 1958

Description. The shell is brown, pyriform, with the sides usually tapering evenly to the aperture (Figs. 1a & d), although the occasional specimen may be slightly mis-aligned or

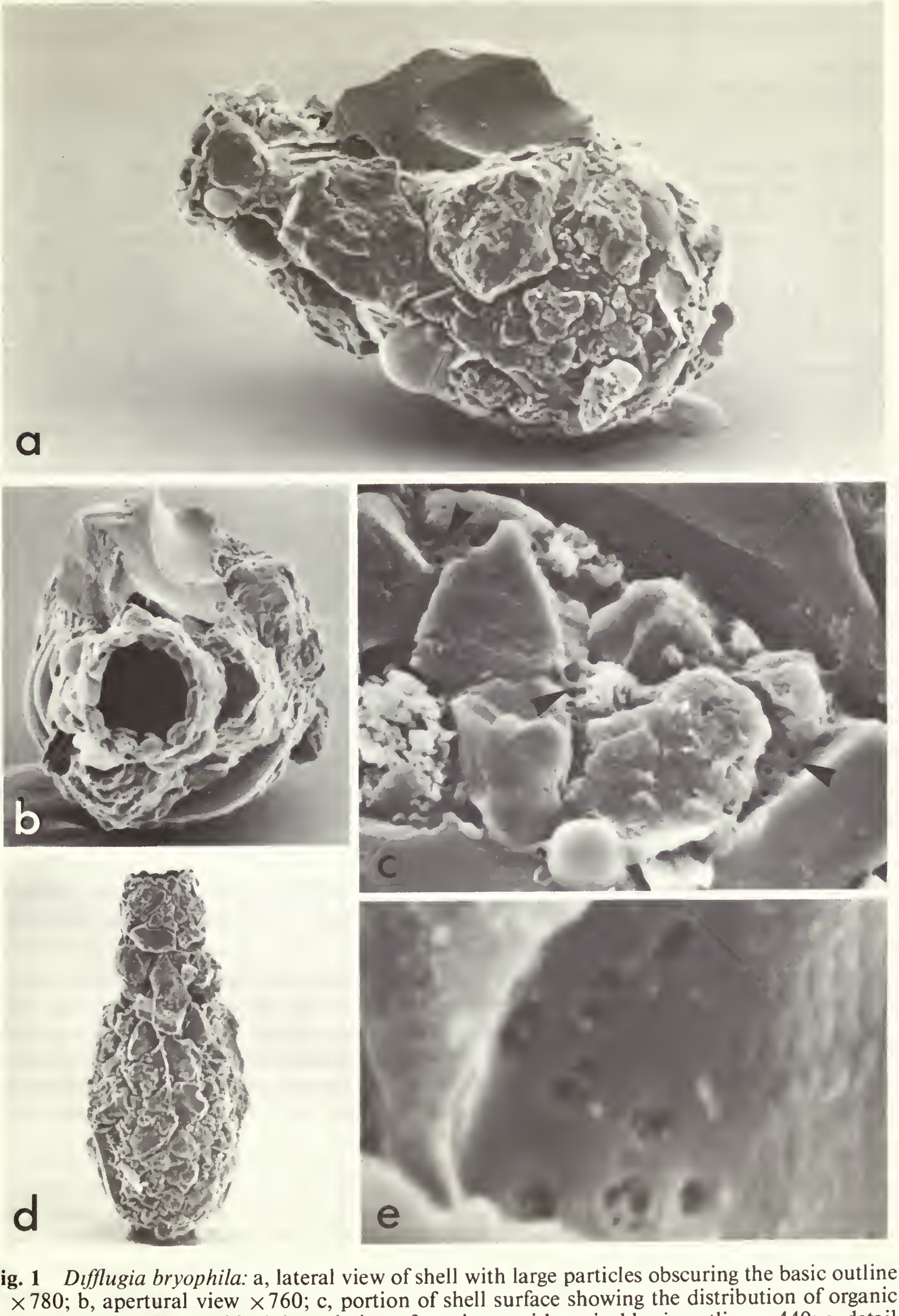

Fig. 1 *Difflugia bryophila:* a, lateral view of shell with large particles obscuring the basic outline ×780; b, apertural view ×760; c, portion of shell surface showing the distribution of organic cement (arrowed) ×5100; d, lateral view of specimen with typical basic outline ×440; e, detail of organic cement ×24 000.

Table 1 Range of measurements (in µm) of pyriform specimens.

Number of specimens	Species	Length (L)	Breadth (B)	Diameter of aperture (d)	B/L	d/L
3	*D. minutissima*	7–14	6–10	2–3		
11	*D. pulex*	28–43	21–30	7–10	0·78±0·10	0·26±0·04
19	*D. pristis*	33–42	21–31	10–13	0·69±0·08	0·31±0·03
3	*D. glans*	67–74	44–50	19–22		
36	*D. manicata*	60–88	37–54	12–20	0·61±0·04	0·20±0·02
25	*D. tenuis*	60–87	37–50	17–27	0·57±0·06	0·30±0·03
7	*D. linearis*	96–108	32–38	12–13	0·35±0·02	0·12±0·01
21	*D. gassowskii*	91–120	45–55	16–21	0·50±0·05	0·18±0·02
39	*D. bryophila*	83–141	49–67	16–22	0·55±0·07	0·17±0·02
36	*D. petricola*	96–124	61–84	20–31	0·65±0·06	0·23±0·03
*(47)	*(D. petricola)*	(108–151)	(72–99)	(25–36)	(0·62±0·05)	(0·22±0·02)
4	*D. paulii*	119–130	48–54	19–23	0·40±0·01	0·17±0·01
38	*D. lanceolata*	108–155	56–92	22–32	0·51±0·05	0·20±0·02
6	*D. parva*	131–162	61–80	19–27	0·51±0·04	0·17±0·02
23	*D. lacustris*	140–231	63–94	26–42	0·41±0·04	0·18±0·02
22	*D. cylindrus*	186–264	91–130	34–49	0·53±0·05	0·21±0·02
46	*D. viscidula*	165–284	116–215	46–89	0·75±0·09	0·30±0·04

*measurements quoted from an earlier report (Ogden & Fairman, 1979)

have a large particle obscuring the even-tapering (Fig. 1a). It is composed mainly of a mixture of small to medium pieces of quartz and the occasional diatom frustule or siliceous flagellate cyst. In common with most rough, thick shells, organic cement is seen infrequently (Fig. 1c), it appears as an open network, with a mesh about 350–450 nm in diameter. The walls of the mesh are not pronounced but blend with the matrix, the mesh openings are often covered by inner strands of cement which appear to form a smaller mesh (Fig. 1e). The aperture is circular and surrounded by small particles (Fig. 1b), in several of the specimens examined small flagellate cysts had also been incorporated to give an irregular margin.

MEASUREMENTS (in µm). See Tables 1 and 2.

MATERIAL EXAMINED Specimens were collected from samples of *Sphagnum* moss gathered at Mately Bog, Lyndhurst, New Forest, Hampshire in March, 1980 and at Mynnd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

GEOGRAPHICAL DISTRIBUTION. Algeria (Gauthier-Lièvre & Thomas, 1958), Belgium (Chardez & Gaspar, 1976; Couteaux, 1969), British Isles (Cash *et al.*, 1919), Chile (Jung, 1942), Congo (Chardez, 1964), Czechoslovakia (Rosa, 1957), France (Thomas, 1954), Gambia (Decloitre, 1947), Germany (Jung, 1936), Roumania (Godeanu *et al.*, 1973), Russia (Kourov, 1925), Spain (Gracia, 1972*a*), Switzerland (Penard, 1902), Tunisia (Gauthier-Lièvre & Thomas, 1958), West Africa (Decloitre, 1948).

REMARKS. This description is in good agreement with Penard (1902) who stated that the sides were rather straight and that it was formed of stones which were usually large and angular.

Amongst the sample from Matley Bog were specimens of *Pontigulasia* which were indistinguishable in size and shape from those of *D. bryophila.* Observations of the former specimens by optical microscopy to determine the presence of an inner diaphragm, the distinguishing generic character for *Pontigulasia,* are often difficult. However, detailed examination by scanning electron microscopy showed that, unless the apertural opening is blocked, it was easy to identify the inner diaphragm and that additionally there are differences in their organic cement patterns (a review of the genus *Pontigulasia* is in preparation).

The random selection of these specimens from the sample gave a ratio of 3 : 1 in favour of *D. bryophila*.

Difflugia cylindrus (Thomas, 1953) comb. nov.

Difflugia oblonga var. *cylindrus* Thomas, 1953

Description. The shell is usually opaque, cylindrical, tapering evenly from the aboral region to the aperture (Fig. 2a). It is composed mainly of medium to large pieces of quartz with the occasional diatom frustule on the rough surface, but the latter are seldom incorporated into the thick structure. Small areas of organic cement in the form of a network are seen infrequently (Fig. 2d). Each mesh of the network is between 300–500 nm in diameter, has thick walls and is covered by a thin perforated layer of cement, the pores of which are evenly distributed and are about 30 nm in diameter (Figs. 2e & f). The aperture is irregular in both outline and composition, being roughly circular and usually surrounded by small particles but often incorporating medium particles that produce a jagged margin (Fig. 2b & c).

Measurements (in µm). See Tables 1 and 2.

Material examined. Specimens were collected from a sample of aquatic plants taken at the banks of the River Brett, near Hadleigh, Suffolk in August, 1979.

Geographical distribution. Algeria (Gauthier-Lièvre & Thomas, 1958), Austria (Laminger, 1973*b*, 1975, 1976), Belgium (Chardez, 1980; Chardez & Gaspar, 1976), Congo (Chardez, 1964), France (Thomas, 1953, 1954; Thomas & Mabille, 1956), Germany (Voeltz-Höhn, 1971), Ivory Coast (Gauthier-Lièvre & Thomas, 1958), Morocco (Gauthier-Lièvre & Thomas, 1958), Poland (Moraczewski, 1965).

Remarks. This species was initially described by Thomas (1953) as a new variety of *D. oblonga,* he also listed what he considered to be previous descriptions of this variety under the general descriptions of *D. oblonga* given by earlier workers. These are not repeated here, but suggest that this variety may be found throughout Europe. The shape, structure and size of the shell, together with the distinct patterning of the organic cement matrix as described above, are considered to be good specific characters sufficient to warrant the raising of this variety to species rank.

Difflugia gassowskii nom. nov.

Difflugia pyriformis longicollis Gassowsky, 1936
Difflugia longcollis (Gassowsky, 1936) Ogden & Hedley, 1980

Description. The shell is pyriform, with a distinct short neck about one-third of the body length, and a rounded aboral region (Fig. 3a). It is rough and composed of small to medium angular pieces of quartz, small areas of organic cement are sometimes seen between particles (Fig. 3b). The cement is in the form of a network, the mesh of which is about 400–550 nm in diameter and the walls 125–200 nm thick, each mesh enclosure has a covering with small perforations about 50 nm in diameter (Fig. 3c). The aperture is circular.

Measurements (in µm). See Tables 1 and 2.

Material examined. Specimens were collected from samples of *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980 and at Clocaenog Forest, Denbigh, Clwyd, North Wales in August, 1980.

Geographical distribution. Belgium (Chardez, 1980; Couteaux, 1969), British Isles (Ogden & Hedley, 1980), Germany (Voeltz-Höhn, 1971), Netherlands (Hoogenraad & Groot, 1940a), Nigeria (Gauthier-Lièvre & Thomas, 1958), Poland (Moraczewski, 1961, 1965), Roumania (Godeanu *et al.,* 1973), Russia (Gassowsky, 1936), Spain (Gracia, 1972*a*; Margalef, 1955).

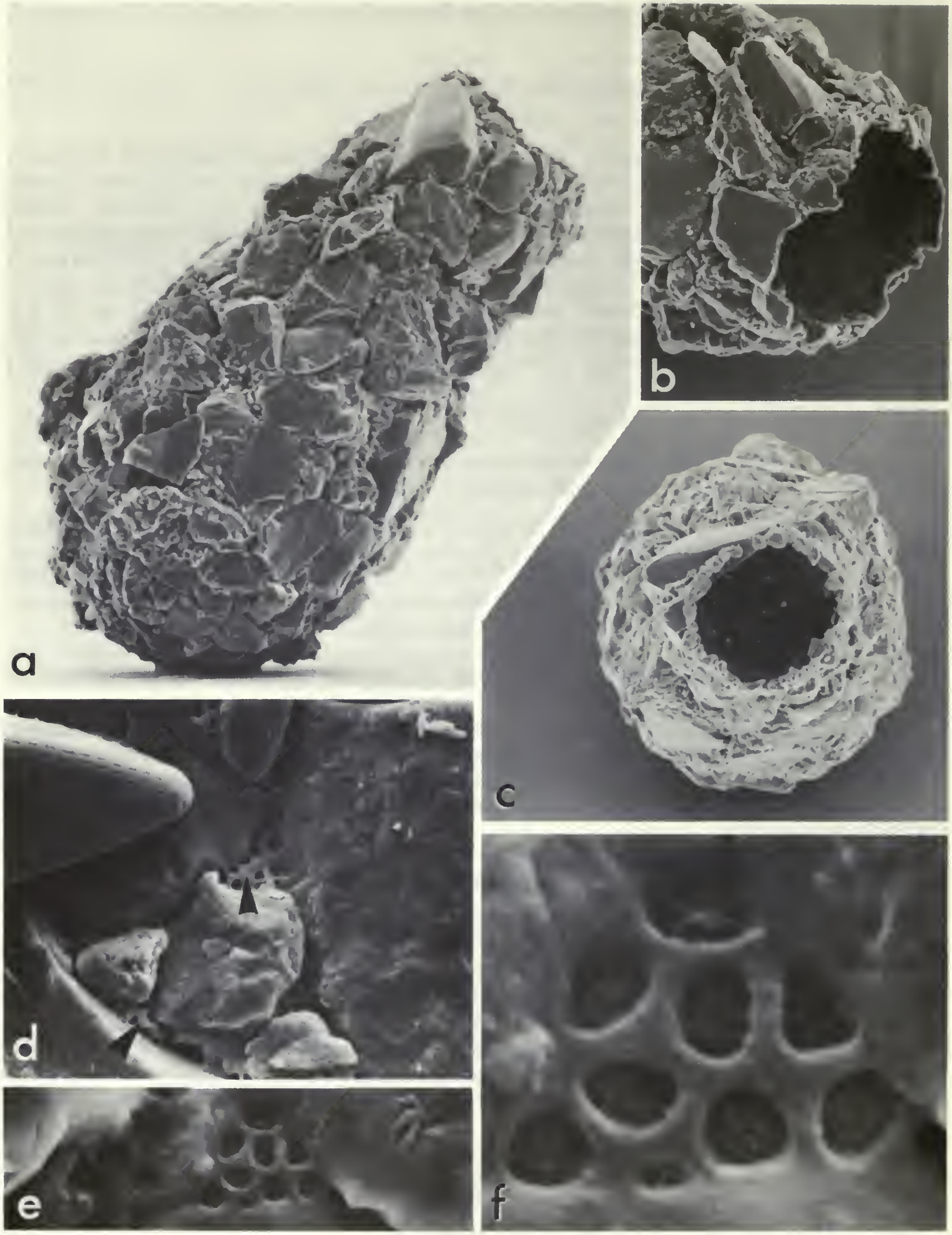

Fig. 2 *Difflugia cylindrus:* a, lateral view ×450; b, side view of aperture to illustrate the irregular margin ×770; c, apertural view ×410; d, shell surface with areas of organic cement (arrowed) ×4200; e, typical arrangement of organic cement network ×8700; d, detail of organic cement ×27 000.

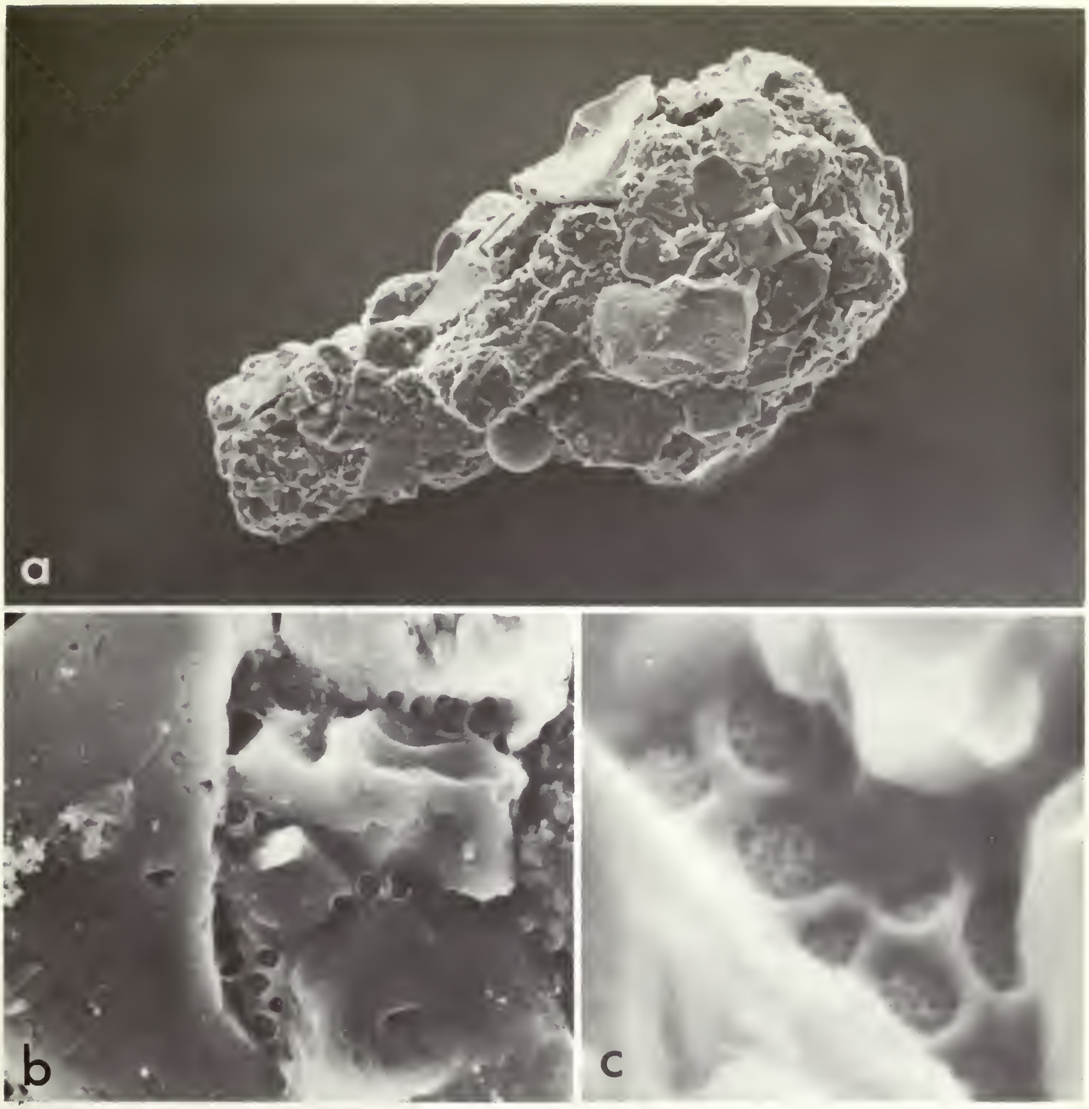

Fig. 3 *Difflugia gassowskii:* a, lateral view ×810; b, shell surface with small areas of organic cement ×7600; c, detail of organic cement network ×24 000.

Remarks. This species has been redescribed recently (Ogden & Hedley, 1980), but is included here on two counts, the added detail of the organic cement and the change of name. The name *D. longicollis* was used initially by Ehrenberg (1854) to describe specimens which now are not considered to belong to the genus *Difflugia,* nevertheless, under the Rules of Zoological Nomenclature the name is preoccupied. I am grateful to Dr. E. G. Merinfeld, Dalhousie University, Halifax, Nova Scotia, for drawing my attention to this point.

Entymology. This species is named after Dr G. N. Gassowsky who first described it from the Karéliens Lakes.

Difflugia glans Penard, 1902

Description. The shell is dark, elongate ovoid, tapering towards the aperture and evenly rounded aborally (Fig. 4a). It is composed mainly of small to medium pieces of quartz,

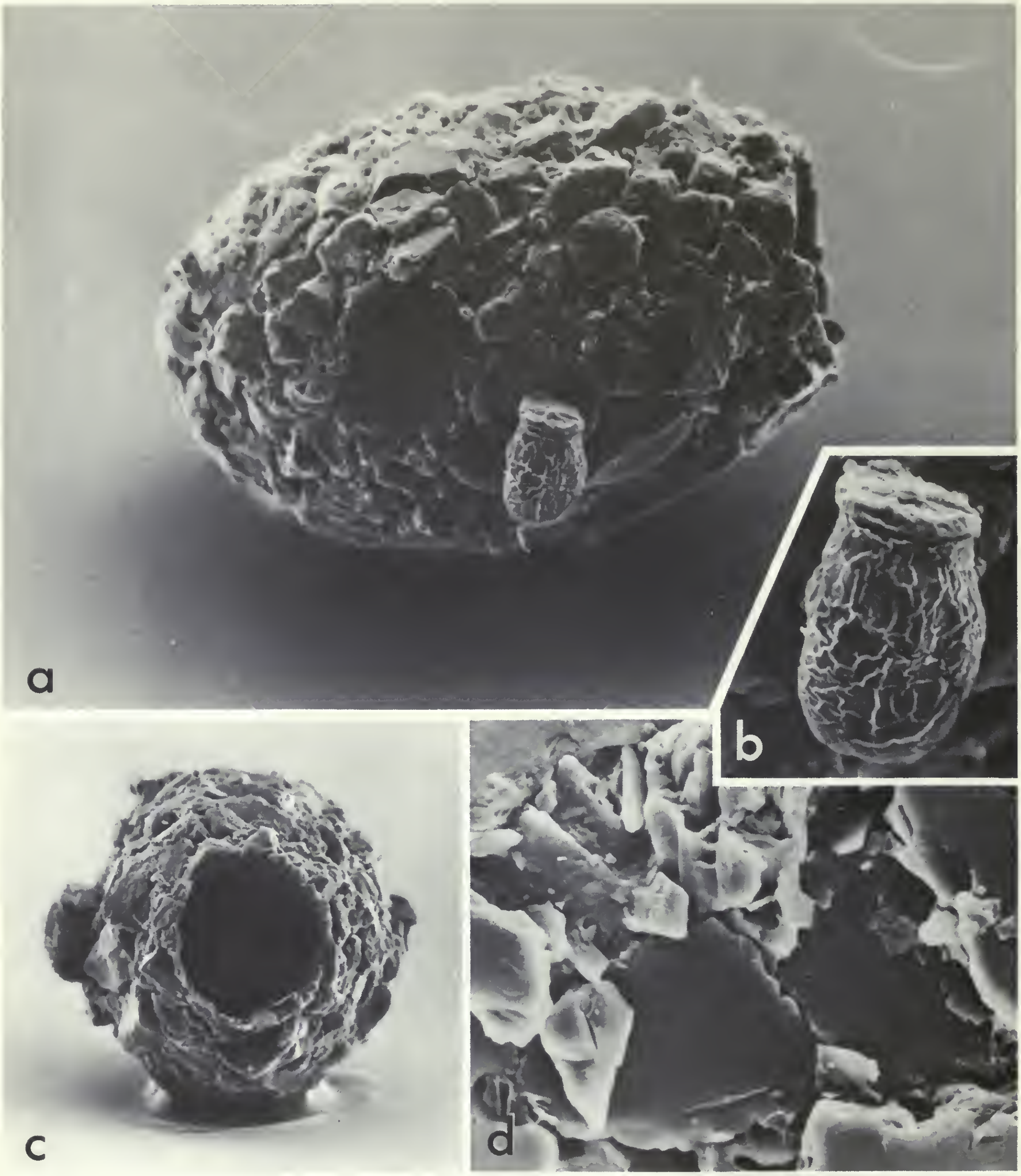

Fig. 4 *Difflugia glans:* a, lateral view ×1400; b, detail of small unidentified cyst ×3000; c, apertural view ×1000; d, portion of shell surface showing the close packing of particles ×3500.

packed closely together with only a minimum amount of organic cement visible (Fig. 4d). A small cyst, of unknown origin, is seen adhering to the surface of the illustrated specimen (Fig. 4b), otherwise the outline is usually well defined. The aperture is circular and surrounded by both small and medium particles (Fig. 4c).

MEASUREMENTS (in µm). See Tables 1 and 2.

MATERIAL EXAMINED. Specimens were collected from a sample of water plants taken at the banks of the River Brett, near Hadleigh, Suffolk in August, 1979 and a gathering of *Sphagnum* moss from Mynnd Hiraethog, Clwyd, North Wales in August, 1980.

Geographical distribution. Austria (Laminger, 1973*b*), Congo (Chardez, 1964), Czechoslovakia (Rosa & Lhotsky, 1971; Štěpánek, 1952), Germany (Jung, 1936; Schönborn, 1962), Italy (Grandori & Grandori, 1934; Rampi, 1950), Russia (Kourov, 1925).

Remarks. This species has not been widely reported, which may be because it falls within the range of three more common species namely, *D. penardi, D. manicata* and *D. rubescens*. It differs from these three species in being a distinct ovoid shape, from *D. rubescens* in being dark and not transparent—although Penard's description of a thin, fragile shell for *D. glans* does not seem compatible with a dark structure which usually suggests that it is robust and strong—and from *D. penardi* and *D. manicata* in aperture size and shape.

Difflugia lacustris (Penard, 1899) comb. nov.

Difflugia pyriformis var. *lacustris* Penard, 1899
Difflugia oblonga var. *lacustris* Cash & Hopkinson, 1909

Description. The shell is transparent or hyaline, elongate, cylindrical or slightly pyriform (Figs. 5a & b). It is composed of small to medium pieces of quartz, diatom frustules and small siliceous flagellate cysts blended together to form a thin structure intermediate between smooth and rough. Only small areas of organic cement occur at the junction of the shell components (Fig. 5d). The cement is in the form of thick-walled rings, between 700–800 nm in diameter, perforated with either three or four holes, 120–160 nm in diameter, which gives these units a similar shape to a button (Fig. 5e). The cement may occasionally be seen either as rings with a slight indentation or as a network of joined rings. When organised as a network the walls of individual rings may be fused together but the typical button-like form are usually seen at the edges. The aperture is usually circular and surrounded by small particles so that the margin is smooth (Fig. 5c).

Measurements (in µm). See Tables 1 and 2.

Material examined. Specimens were collected from three samples in the same locality, aquatic plants at the edge of a pond in Burley, and two gatherings of *Sphagnum* from opposite banks of a small stream at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980.

Geographical distribution. Algeria (Gauthier-Lièvre & Thomas, 1958), Argentina (Dioni, 1970; Lena & Zaidenwerg, 1975), Austria (Laminger, 1973*b* 1974, 1975), Belgium (Chardez, 1980; Chardez & Gaspar, 1976; Oye, 1953), British Isles (Cash & Hopkinson, 1909), Congo (Chardez, 1964; Gauthier-Lièvre & Thomas, 1958), Czechoslovakia (Štěpánek, 1967), France (Thomas, 1954; Thomas & Mabille, 1956), Germany (Jung, 1936; Schönborn, 1962*a* & *b*), Guatemala (Laminger, 1973*a*), Italy (Rampi, 1950), Ivory Coast (Gauthier-Lièvre & Thomas, 1958), Mexico (Laminger, 1973*a*), Morocco (Gauthier-Lièvre & Thomas, 1958), Poland (Moraczewski, 1961, 1965), Roumania (Godeanu *et al.*, 1973), Russia (Kourov, 1925), Switzerland (Penard, 1902), United States of America (Laminger *et al.*, 1979; Wailes, 1912).

Remarks. The specimens described here agree well with the original description (Penard, 1899)—shell long, cylindrical, larger in the rear, rarely with a small constriction of the neck—and those given later by Penard (1902) and Cash & Hopkinson (1909). Nevertheless, it would appear that these earlier descriptions were based on groups of similar specimens, hence Penard's reference to a constriction of the neck and the diverse illustrations provided by Cash & Hopkinson. As a result of the latter diagrams, two specimens were tentatively identified as *D. lacustris* in a previous publication (Ogden, 1980). Additional specimens to

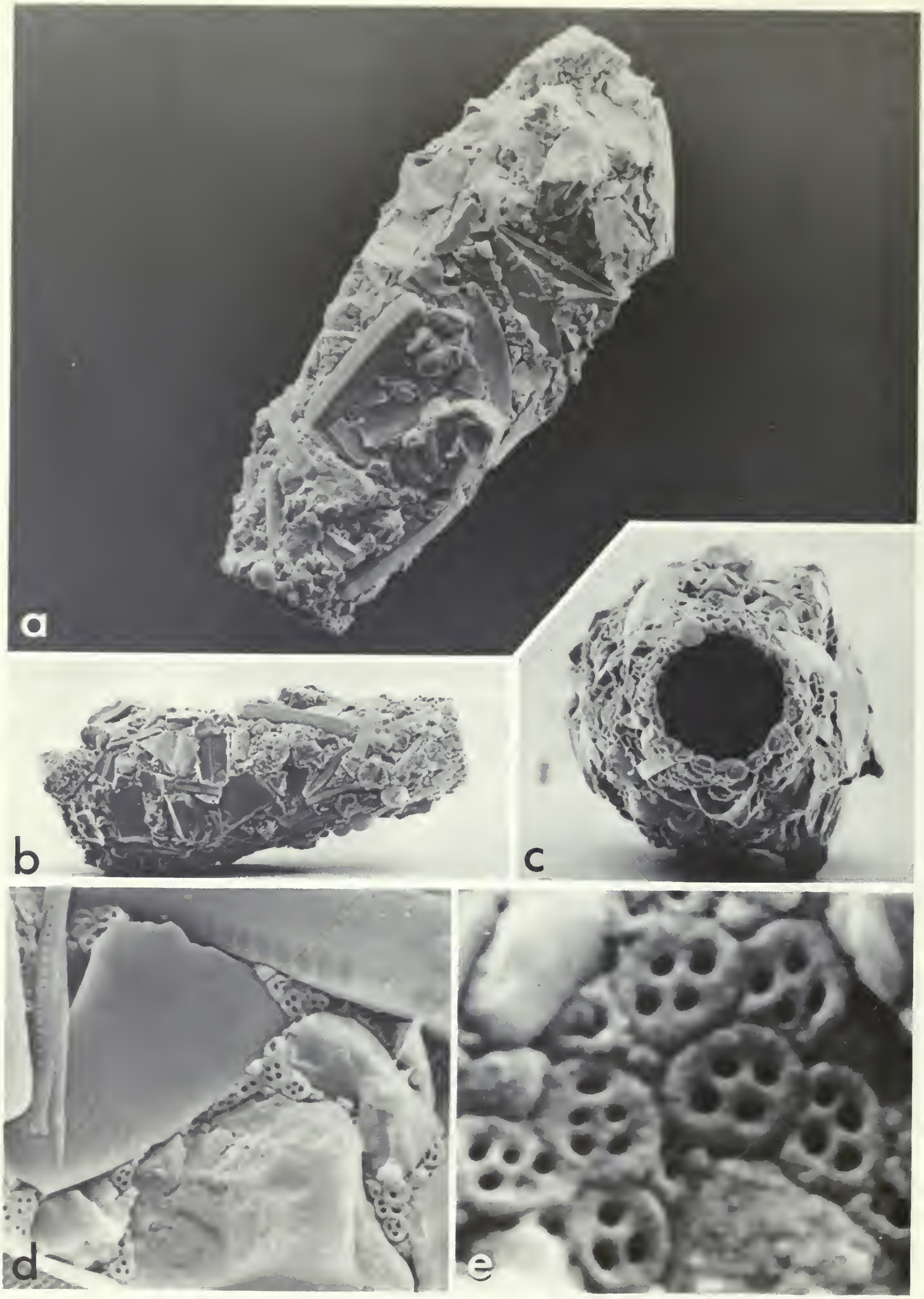

Fig. 5 *Difflugia lacustris:* a, lateral view ×450; b, alternative view of same specimen (a.) to illustrate the uniform shape ×280; c, apertural view ×500; d, shell surface showing the distribution of organic cement ×5800; e, detail of organic cement network ×24 000.

the two mentioned above have been examined and are clearly seen to differ from *D. lacustris*, they are now referred to *D. linearis* (see below).

The present account shows that *D. lacustris* has a well defined shape and a distinctive patterning of organic cement which are considered sufficient to designate this a distinct species.

Difflugia lanceolata Penard, 1890

Description. The shell is yellow or hyaline, lanceolate, tapering from the widest diameter situated about two-thirds of the body-length from the aperture, to give a clean outline that is rounded aborally and evenly angled towards the aperture (Fig. 6a). It is composed of small to medium flattish pieces of quartz and some flat diatom frustules so arranged that the shell is thin and smooth, the surface frequently appearing as though it had been polished, a feature that often permits easy identification. An angular piece of quartz may occasionally protrude from the surface but these are uncommon and limited to one or two in any one shell. As the shell components are usually arranged so that they are in close contact with each other there are no large areas of organic cement, nevertheless, a network of small rings of organic cement may be seen between these particles (Figs. 6d, e, f). The rings are 240–300 nm in diameter and have a distinct wall about 150–200 nm in thickness with a smooth membrane over the mesh. When several rings fuse to form a sheet the thick wall is still usually apparent. The aperture is circular and well defined because the rim has a thin covering of organic cement (Figs. 6b & c).

Variation appears to be limited to cigar-shaped specimens which have almost parallel sides, one such specimen is illustrated by Ogden & Hedley (1980).

Measurements (in µm). See Tables 1 and 2.

Material examined. The majority of specimens came from a sample of *Sphagnum* moss collected close to a small stream at Holmsley Lodge, Burley, New Forest, Hampshire, a few came from a similar sample on the opposite bank where they were equally abundant, both samples were taken in March, 1980.

Geographical distribution. Argentina (Vucetich, 1973*a, b*), Austria (Laminger, 1972*c*), Belgium (Chardez, 1961; Oye, 1953), Brazil (Green, 1975), British Isles (Cash & Hopkinson, 1909; Ogden & Hedley, 1980), Canada (Decloitre, 1965), China (Decloitre, 1965), Congo (Chardez, 1964), Czechoslovakia (Opravilová, 1974), France (Thomas, 1954; Thomas & Mabille, 1956), Germany (Schönborn, 1975), Hungary (Gal, 1969), Java (Bartoš, 1963*a*), Morocco (Gauthier-Lièvre & Thomas, 1958), Poland (Golemansky, 1970; Moraczewski, 1961, 1965), Roumania (Godeanu *et al.,* 1973), Sudan (Gauthier-Lièvre & Thomas, 1958), Switzerland (Penard, 1902), Venezuela (Grospietsch, 1975), West Africa (Decloitre, 1965), United States of America (Decloitre, 1965).

Remarks. The organic rim surrounding the aperture is shared with one other pyriform species of *Difflugia,* namely *D. rubescens* where the cement is in the form of tooth-like projections (see Pl.66 *in* Ogden & Hedley, 1980). The only other species of which we are aware that has an organic rim is *D. oviformis,* but this was transferred to a new genus *Netzelia* by Ogden, 1979. *D. lanceolata* is characterized by its uniform size and outline.

Difflugia linearis (Penard, 1890) Gauthier-Lièvre & Thomas, 1958

Difflugia oblonga var. *linearis* Penard, 1890
Difflugia lacustris in Ogden, 1980

Description. The shell is transparent, flask-shaped or elongate pyriform, having a long thin neck with parallel sides and a slightly swollen, rounded aboral region (Fig. 7a). The surface is sometimes slightly uneven because of projecting particles, but generally it has a regular

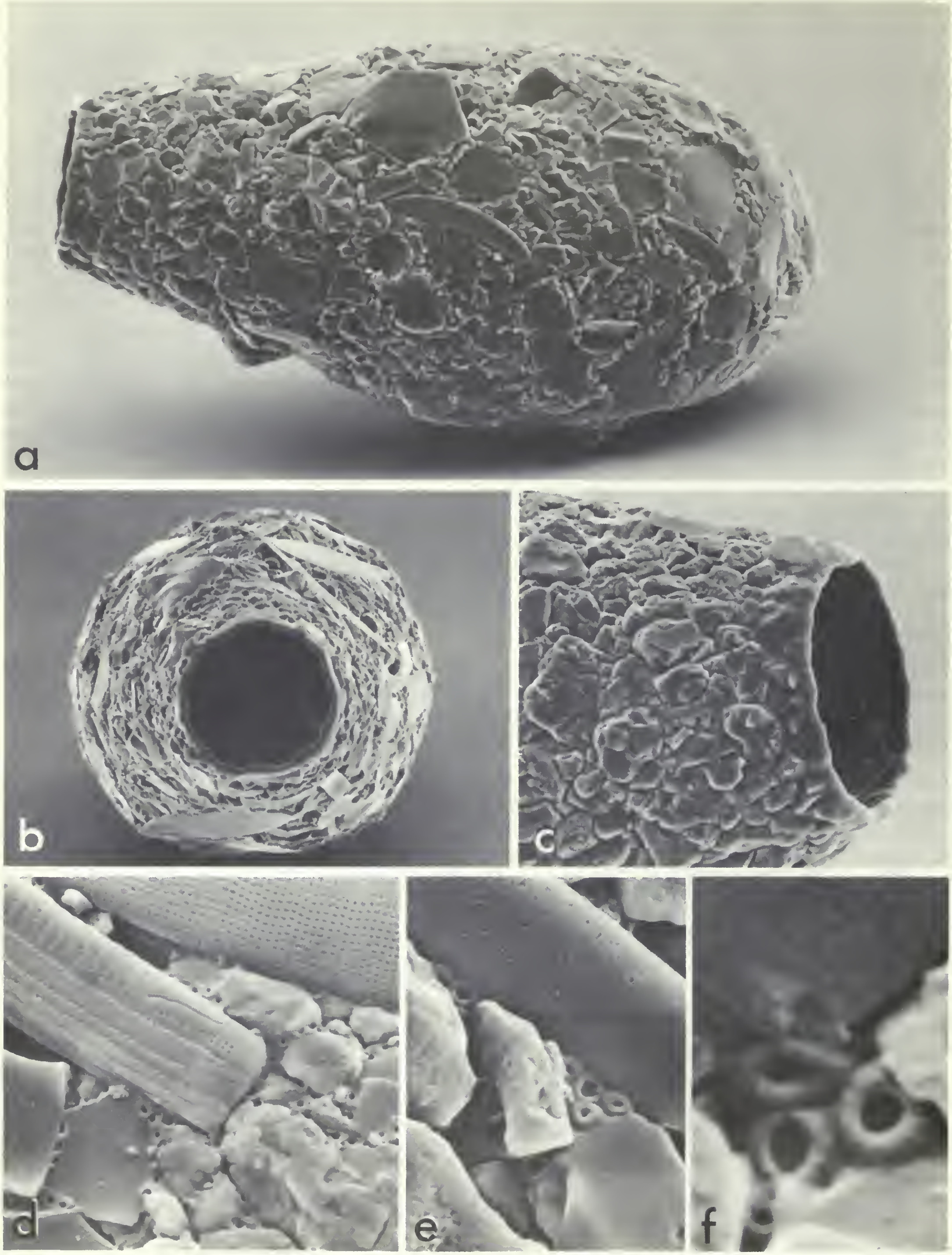

Fig. 6 *Difflugia lanceolata:* a, lateral view ×930; b, apertural view ×760; c, side view of aperture to illustrate the thin covering of organic cement around the rim ×1500; d, shell surface with small isolates of organic cement ×4400; c, small rings of organic cement between particles ×7600; f, detail of organic cement ×24 000.

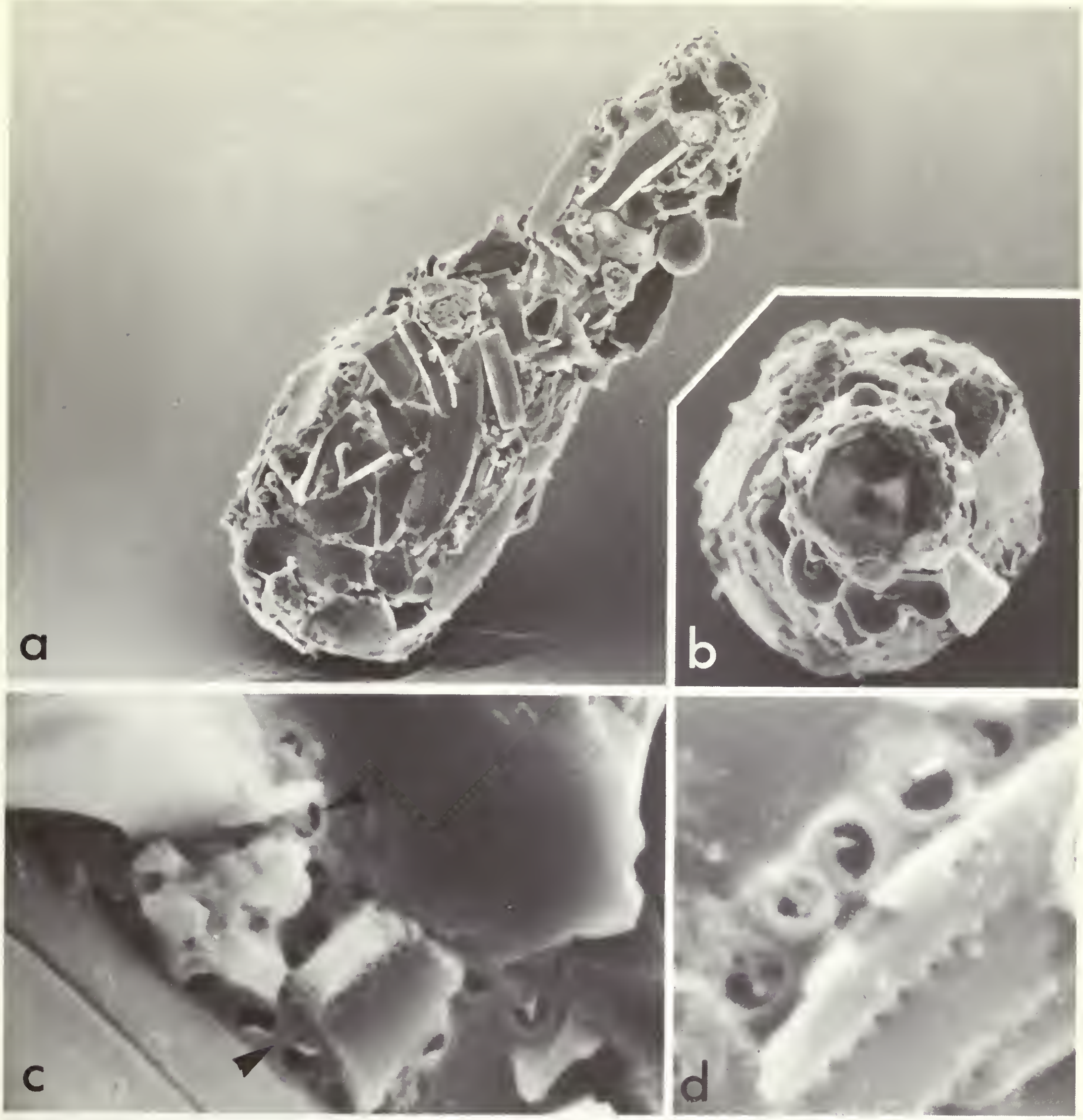

Fig. 7 *Difflugia linearis:* a, lateral view ×950; b, apertural view ×1200; c, portion of shell surface showing areas of organic cement (arrowed) ×14 000; d, detail of organic cement ×24 000.

outline. It is composed of a mixture of flattened pieces of quartz, small whole, flat diatom frustules, fragments of flattish frustules, small siliceous shell plates and round flagellate cysts. Small areas of organic cement, in the form of a network with an open mesh, are occasionally seen (Fig. 7c), The open mesh has a diameter of about 300 nm and walls 100 nm thick (Fig. 7d). In appearance, the openings of the mesh suggest that it may have been covered at some time and has subsequently been broken, but only the examination of further specimens will establish its normal condition. The aperture is circular and usually surrounded by small particles (Fig. 7b).

Measurements (in µm). See Tables 1 and 2.

Material examined. Specimens were collected from *Sphagnum* moss gathered at Holmsley

Lodge, Burley, New Forest, Hampshire on two occasions, May, 1978 and March, 1980, and at Myndd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

GEOGRAPHICAL DISTRIBUTION. Austria (Laminger, 1973*b*, 1975), Belgium (Chardez, 1961*b*), British Isles (Ogden, 1980), Bulgaria (Golemansky, 1967), Congo (Chardez, 1964), France (Thomas, 1954), Germany (Penard, 1890), Ivory Coast (Gauthier-Liévre & Thomas, 1958), Nepal (Laminger, 1972*b*), Roumania (Godeanu *et al.*, 1973).

REMARKS. The initial description of this species (Penard, 1890) was brief, and relies mainly on the diagrams. The scarcity of subsequent reports may be due to this inadequate description or the difficulty in finding this species, which by being thin, long and transparent

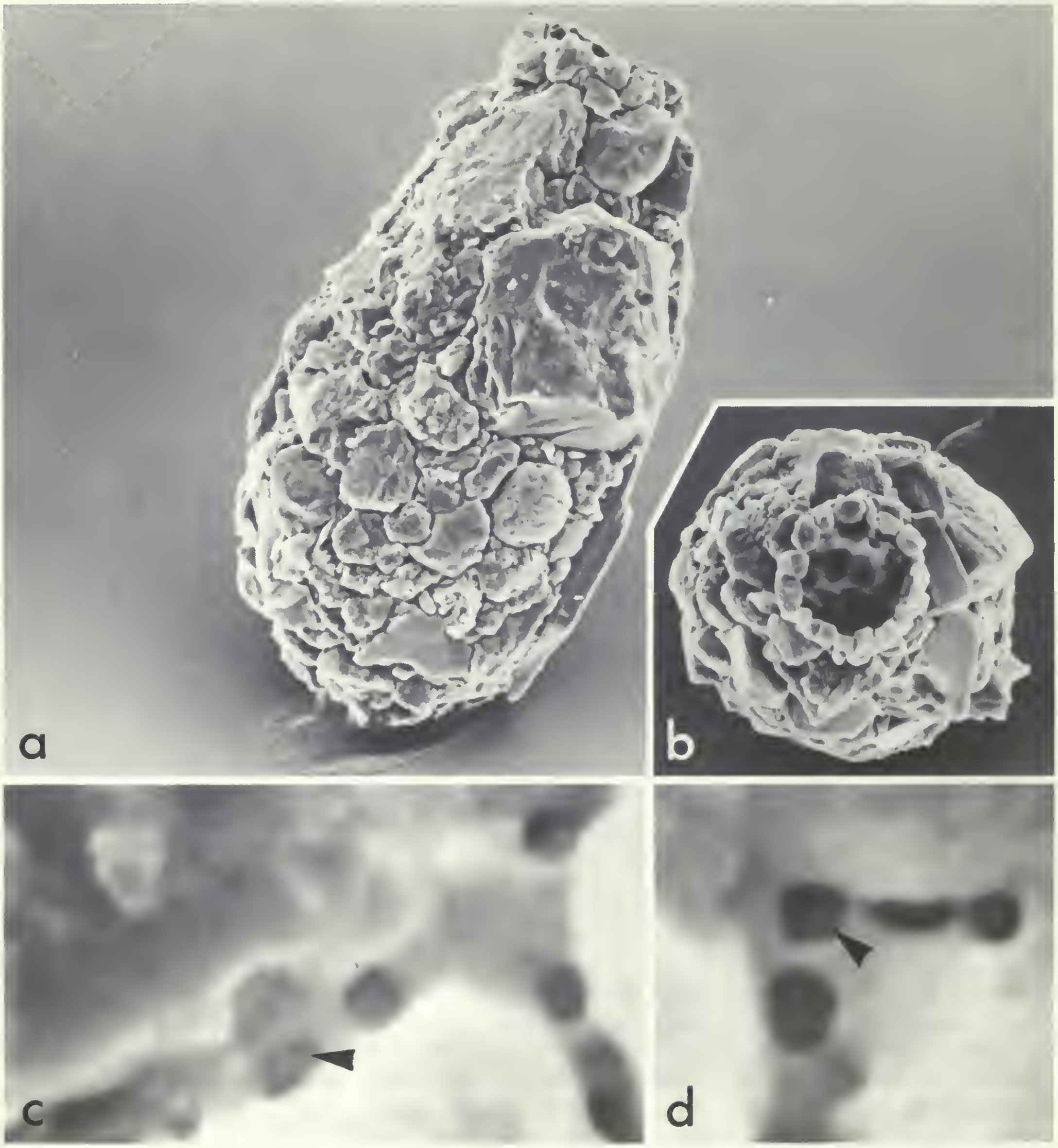

Fig. 8 *Difflugia manicata:* a, lateral view × 1300; b, apertural view × 1100; c, and d, detail of organic cement with the ill-defined inner structure (arrowed) × 30 000.

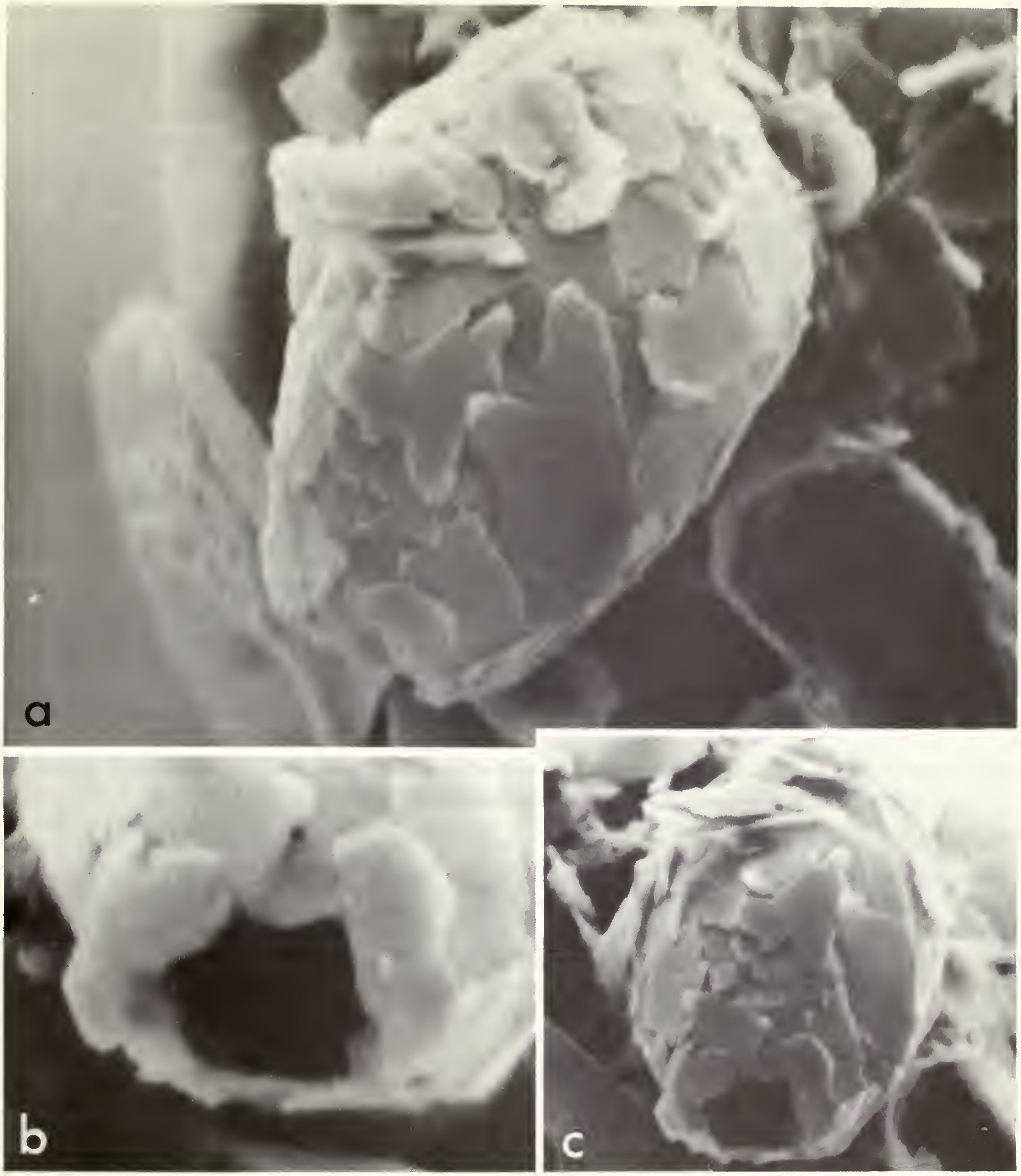

Fig. 9 *Difflugia minutissima:* a, lateral view to show the arrangement of flattish particles ×6700; b, detail of aperture × 10 000; c, latero-apertural view ×4900.

makes it unusually elusive. Two specimens described earlier (Ogden, 1980) and tentatively identified as *Difflugia lacustris,* because of their similarity to the description given by Cash & Hopkinson (1909) and especially to one figure (Pl. XIX Fig. 1), are now redescribed as *D. linearis*. Additional specimens, plus the benefit of being able to compare these with specimens of *D. lacustris* (see p. 9), allows the former identification to be rectified and show that *D. linearis* is a distinct species.

Difflugia linearis can be differentiated from other pyriform species by its distinctive flask-like shape, thin, transparent shell and small aperture.

Difflugia manicata Penard, 1902

Description. The shell is yellow or brown, pyriform, tapering evenly and gradually from a rounded aboral extremity towards the aperture (Fig. 8a). The surface is rough and composed mainly of small to medium pieces of quartz, although the occasional specimen may have large particles added. Small areas of organic cement are seen infrequently, due to the close packing of the shell material, but when present they appear either as strands or as pores in a matrix (Fig. 8c). These pores are about 300 nm in diameter and have an ill-defined inner structure which appears to have smaller pores about 130 nm in diameter (Figs. 8c & d). The aperture is circular and surrounded by a distinct pattern of small particles (Fig. 8b).

Measurements (in µm). See Tables 1 and 2.

Material examined. Specimens were collected from samples taken at three sites, *Sphagnum* moss gatherings at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980 and Mynnd Hiraethog, Clwyd, North Wales in August, 1980, and from aquatic plants taken at the banks of the River Brett, near Hadleigh, Suffolk in August, 1979.

Geographical distribution. Austria (Laminger, 1971, 1972*c*), Belgium (Chardez, 1961*b*), British Isles (Cash *et al.,* 1919; Ogden & Hedley, 1980), Congo (Štěpánek, 1963), Italy (Grandori & Grandori, 1934), Poland (Moraczewski, 1965; Pateff, 1926, 1927), Switzerland (Penard, 1902).

Remarks. Although this species was thought to be uncommon by Cash, Wailes & Hopkinson (1919), it is suggested that this has been one of the overlooked species and that it will probably be found as one of the most commonly distributed. The wide range of habitat already reported, lake, river and *Sphagnum* moss would appear to support this opinion.

Difflugia minutissima Penard, 1904

Sexangularia minutissima (Penard, 1904) Deflandre, 1931

Description. The shell is transparent, elongate or ovoid, rounded aborally and tapering slightly towards the aperture (Figs. 9a & c). It is composed of thin flattish pieces of quartz, and the occasional diatom frustule, which are arranged so that they overlap, but the result is still a fragile structure. Only small strands of organic cement have been seen at some junctions. The aperature is basically circular, any variation is usually due to the irregular arrangement of particles around the opening (Fig. 9b).

Measurements (in µm). See Tables 1 and 2.

Materials examined. Specimens were collected from a sample of *Sphagnum* moss gathered at Mynnd Hiraethog, Clwyd, North Wales in August 1980.

Geographical distribution· Switzerland (Penard, 1904)

Remarks. This species appears to be known only from the initial description (Penard, 1904), although Deflandre (1931) using Penard's description suggested that it should be transferred to the genus *Sexangularia* Awerintzew, 1906. The main features of this latter genus are 'chitinous shell, with or without the addition of extraneous particles; polygonal in transverse section, most often hexagonal'. At present it is considered that these features are insufficient to differentiate this genus from *Difflugia,* and therefore refer the included species to *Difflugia–D. minutissima* Penard, 1904; *D. parvula* (Awerintzew, 1906) and *D. polydera* Deflandre, 1931.

The specimens described here were found adhering to extraneous particles when prepared by air-drying and because of this it is not possible to examine them in transverse section, nevertheless, they do not appear to be polygonal. The value of this feature in relation to a fragile shell is questionable, especially as Penard's observations would have been carried out on specimens under a cover slip, which would allow a degree of compression. The specimens share similar dimensions to those given by Penard for *D. minutissima* and are so designated.

Difflugia parva (Thomas, 1954) comb. nov.

Difflugia oblonga var. *parva* Thomas, 1954

DESCRIPTION. The shell is pyriform, tapering evenly from the swollen and rounded aboral third, to the aperture for the remaining two-thirds (Fig. 10a). It is composed mainly of a mixture of small to medium pieces of quartz, often with the addition of two or three large pieces. Organic cement is seen between particles usually as a series of single units (Fig. 10c), which may overlap but are seldom fused to form a network. Each unit is a ring about 650–750 nm in external diameter, 300–380 nm internal diameter, with walls about 150 nm thick. A small mesh covers the inner portion of each ring (Fig. 10d). The aperture is circular and surrounded mainly by small particles (Fig. 10b).

MEASUREMENTS (in µm). See Tables 1 and 2.

MATERIAL EXAMINED. Specimens were collected from *Sphagnum* moss gathered at Matley Bog, Lyndhurst, New Forest, Hampshire in March, 1980; Mynnd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980 and aquatic plants from a pond at Burley, New Forest, Hampshire in March, 1980.

GEOGRAPHICAL DISTRIBUTION. Algeria (Gauthier-Lièvre & Thomas, 1958), Argentina (Lena & Zaidenwerg, 1975), Austria (Laminger, 1973*b*), Belgium (Chardez, 1980; Chardez & Gaspar, 1976; Couteaux, 1969), Bulgaria (Golemansky, 1967), France (Thomas, 1954; Thomas & Mabille, 1956), Germany (Schönborn, 1965; Voeltz–Höhn, 1971), Ivory Coast (Gauthier-Lièvre & Thomas, 1958), Poland (Golemansky, 1970; Moraczewski, 1965), Venezuela (Grospietsch, 1975).

REMARKS. There have been several reports of *D. oblonga* var. *parva* since Thomas (1954) described his new variety, although size was the only diagnostic feature used and illustrated (Pl. III, Fig. 1) by him to differentiate this variety from *D. oblonga.* The figure given also shows the difference in shell composition, described below as a specific feature.

This variety is considered as a distinct species from *D. oblonga* because of its clean outline, relatively smooth surface and detailed cement pattern.

Difflugia paulii nom. nov.

Difflugia oblonga var. *elongata* Oye, 1953

DESCRIPTION. The shell is transparent, slim and elongate, tapering evenly from just anterior of the mid-body region towards the aperture, the even-tapering is more apparent in Fig. 11b whereas the upper side of Fig. 11a has a misleading hump, the posterior region is slightly swollen, curving sharply and smoothly at the extremity (Fig. 11a). It is composed of flattish pieces of quartz to give a smooth appearance, with small areas of organic cement often apparent as part of the matrix (Fig. 11c). The cement is in the form of small perforated cones about 600 nm in diameter, the perforations being about 100–150 nm in diameter (Fig. 11d). The aperture is circular and surrounded by small pieces of quartz (Fig. 11b).

MEASUREMENTS (in µm). See Tables 1 and 2.

MATERIAL EXAMINED. Specimens were collected from a sample of *Sphagnum* moss gathered at Mynnd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

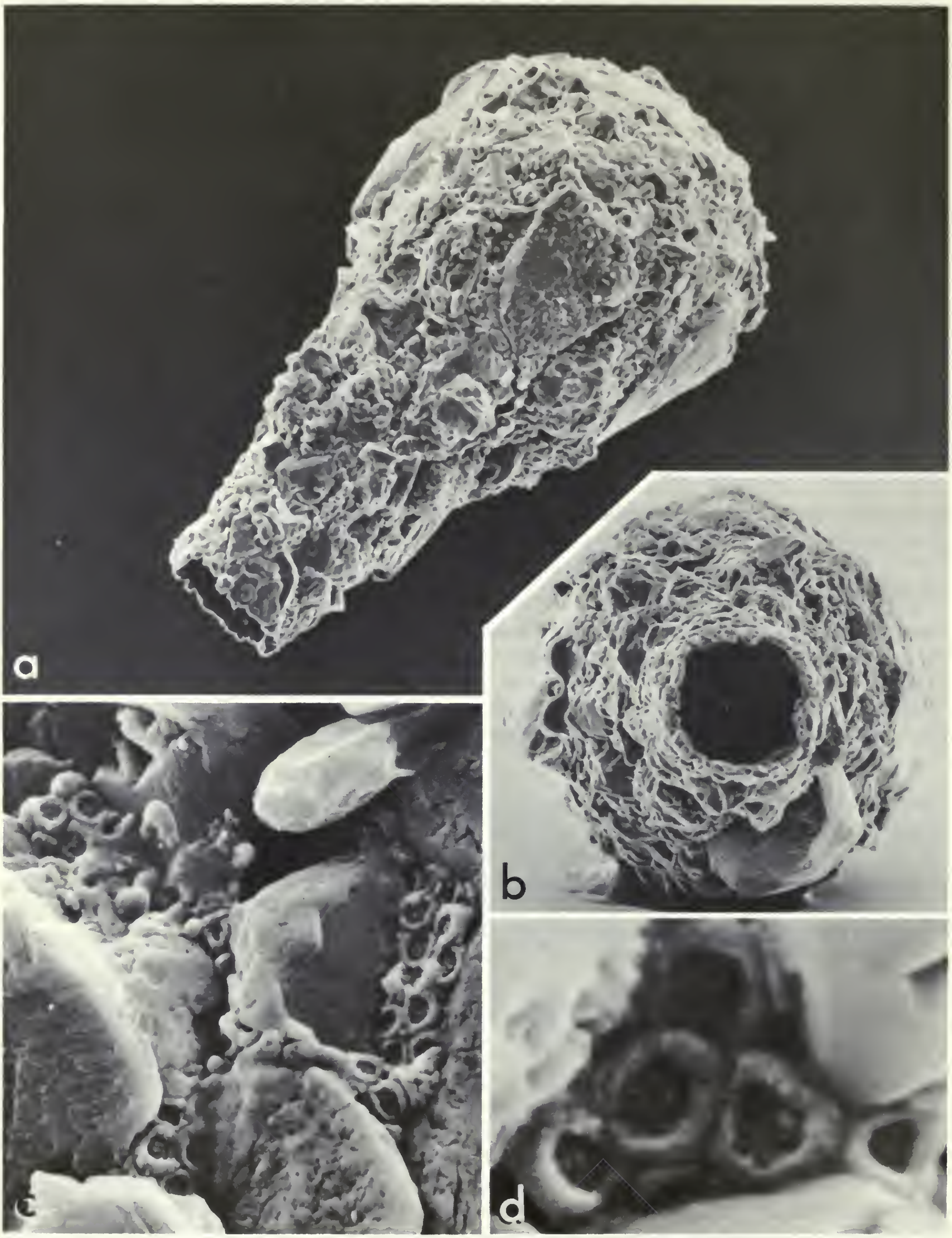

Fig. 10 *Difflugia parva:* a, lateral view ×710; b, apertural view ×790; c, shell surface showing areas of organic cement ×9800; d, detail of organic cement ×30 000.

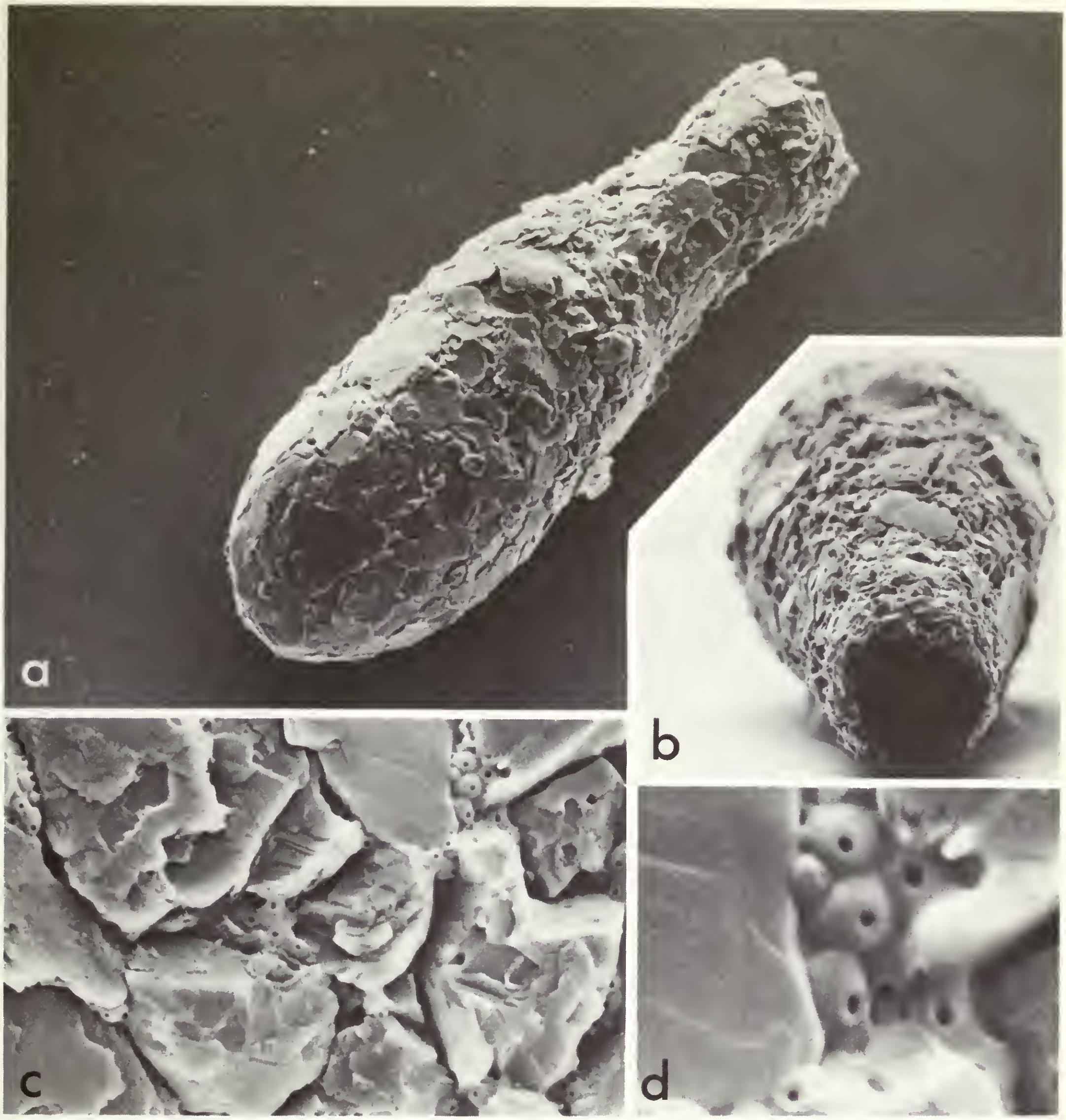

Fig. 11 *Difflugia paulii:* a, lateral view ×800; b, apertural view ×790; c, portion of shell surface ×4600; d, detail of organic cement ×15 000.

Geographical distribution. Austria (Laminger, 1973*b*), Belgium (Oye, 1953), Congo (Gauthier-Lièvre & Thomas, 1958), Spain (Gracia, 1972*a*).

Remarks. This species has been described on two occasions, from Belgium by Oye (1953) and from Africa by Gauthier-Lièvre & Thomas (1958). Oye (1953) stated that these specimens were slender in comparison with *D. lacustris,* and considered that this feature and the limited grains of quartz in the shell was sufficient to warrant a new variety. Gauthier-Lièvre and Thomas (1958) agreed with this earlier description and designation.

Of the more elongated pyriform species, *D. paulii* in body length appears to occupy a position mid-way between *D. linearis* and *D. lacustris,* the present work shows that it is distinct from these two species in outline, elemental composition and patterning of the organic cement, in addition, it can be differentiated from *D. linearis* by the size of the aperture (Table 1).

ETYMOLOGY. This species is named after Dr Paul van Oye whose original description was based on specimens from a pond in Belgium.

Difflugia petricola Cash, 1909

This species has been redescribed recently by Ogden & Fairman (1979). It is reported here only to demonstrate the regularity of dimensions between specimens from different localities, see Tables 1 and 2, because these are often used as taxonomic features.

MATERIAL EXAMINED. Specimens were collected from *Sphagnum* moss gathered at two sites, Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980 and Mynnd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

Difflugia pristis Penard, 1902

DESCRIPTION. The shell is brown or opaque, ovoid, tapering from the mid-body position towards the aperture and gracefully curved aborally (Fig. 12a). It is thin, smooth and composed of flattish pieces of quartz (Fig. 12a-c) or infrequently including flat pieces of diatom frustule. The particles are packed closely together and only small connections of organic cement are visible (Figs. 12d & e). The aperture is circular with a regular margin (Fig. 12b).

MEASUREMENTS (in μm). See Tables 1 and 2.

MATERIAL EXAMINED. Specimens were collected from samples of *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in May, 1978 and at Myndd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

GEOGRAPHICAL DISTRIBUTION. British Isles (Cash & Hopkinson, 1909), Czechoslovakia (Štěpánek, 1967), Hungary (Varga, 1963), Italy (Grandori & Grandori, 1934), Java (Bartoš, 1963*a*), Poland (Moraczewski, 1965), Roumania (Godeanu *et al.*, 1973), Switzerland (Penard, 1902).

REMARKS. Cash and Hopkinson (1909) considered their specimens to be in good agreement with Penard's (1902) description, except for the absence of refractive particles that made the shell appear opaque or black. This they attributed to the difference in habitat of their samples, the former being found amongst floating vegetation in clear water and Penard's from a muddy lake bottom. Some differences in size have been reported since Penard who gave 45–65 μm as the range of length, Cash and Hopkinson gave 60–65 μm, whilst more recently Varga (1963) found specimens measuring 44–48 μm in length.

The specimens reported here are smaller than any previously described, although in all other respects agree with Penard's description. The main features that distinguish *D. pristis* from *D. pulex* are the darker colour and the more regular shape.

A single larger specimen, 56 μm long, 31μm wide, aperture 10 μm in diameter, with the typical pyriform shape (Fig. 13a & b) was found in the sample from Wales. This is reported here as being questionably *D. pristis* (?), being atypical in having a definite neck, the discovery of more specimens may result in a more accurate identification. This specimen is similar to those identified by Cash & Hopkinson (1909) as (?) *D. pulex* which they described as being 'oval, tapering suddenly to a short neck'.

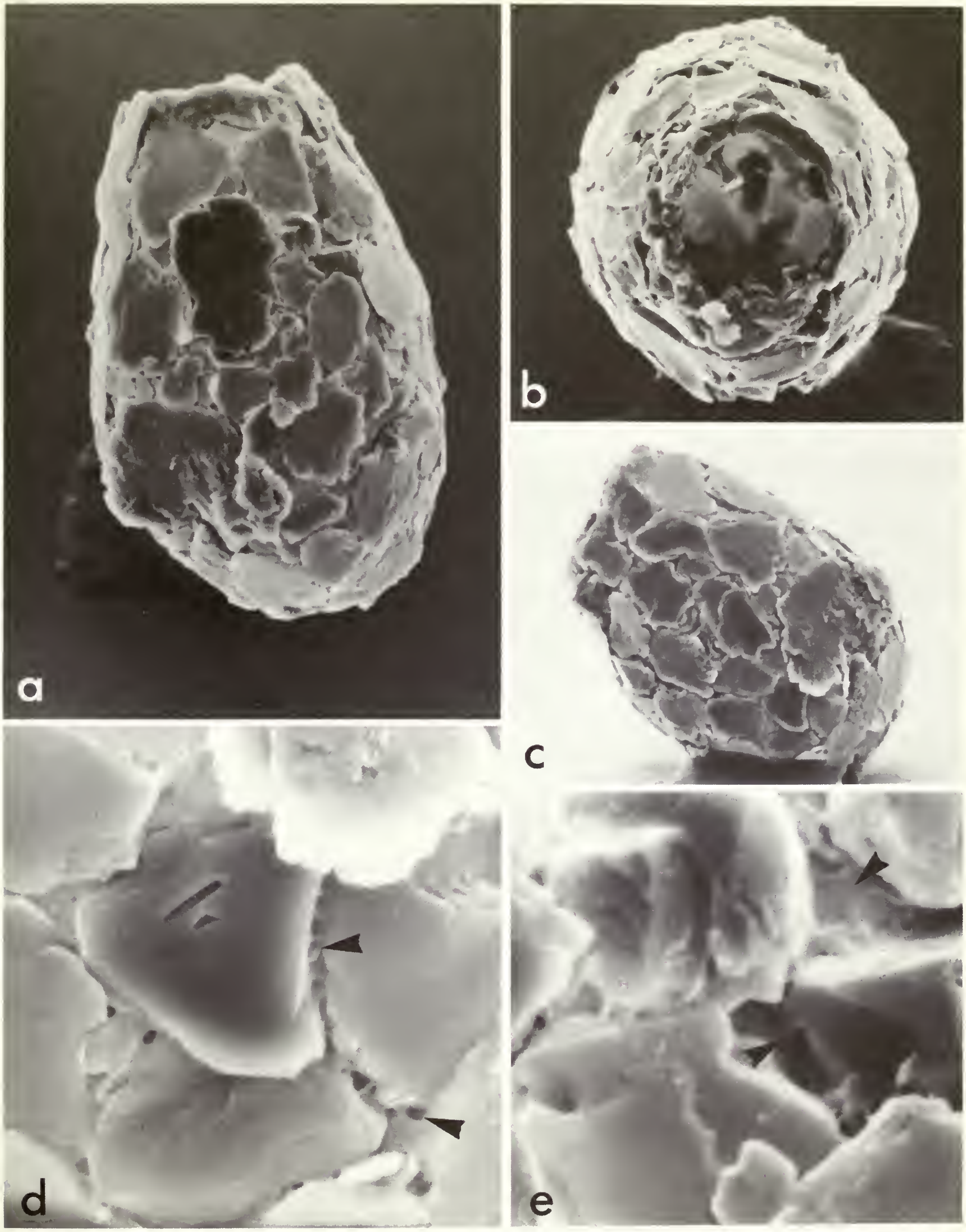

Fig. 12 *Difflugia pristis:* a, lateral view ×2400; b, apertural view ×2400; c, alternative view of specimen shown in a., to illustrate regular ovoid shape ×1700; d and e, portions of shell surface with small connections of organic cement (arrowed) ×9300 and ×14 000.

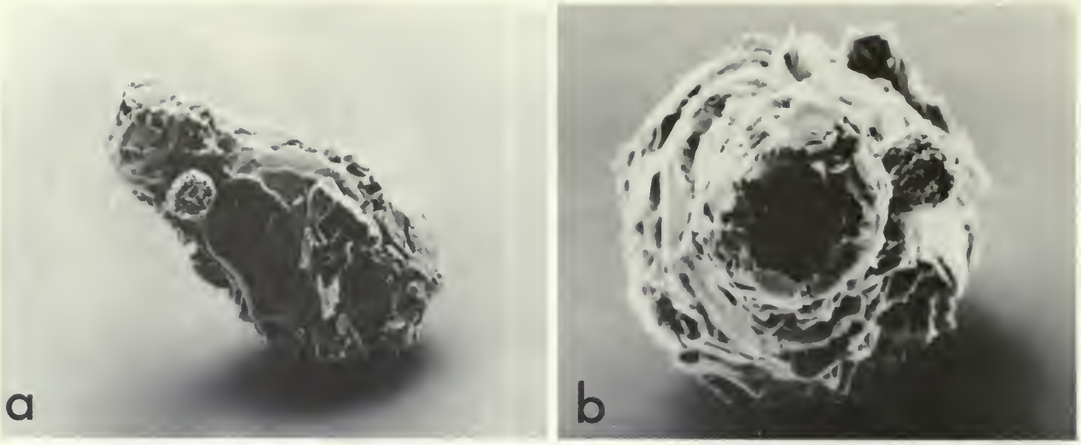

Fig. 13 *Difflugia pristis* (?): a, lateral view to show distinct neck × 860; b, apertural view × 1600.

Difflugia pulex Penard, 1902

Difflugia minuta minor Godeanu, 1972

Description. The shell is transparent, elongate or ovoid (Figs. 14a & d). It is composed mainly of a mixture of small thin pieces of flat quartz and pieces of diatom frustule, often with whole frustules or round flagellate cysts adhering to the surface (Figs. 14a–e). The arrangement of these particles is such that only small strands of organic cement are visible. The aperture is usually circular (Fig. 14c) but may vary due to the arrangement of the surrounding particles (Fig. 14b).

Measurements (in μm). See Tables 1 & 2.

Material examined· Specimens were collected from samples of *Sphagnum* moss gathered at Subberthwaite, Broughton in Furness, Cumbria in June 1979 and at Mynnd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

Geographical distribution· Argentina (Lena & Zaidenwerg, 1975), Australia (Playfair, 1918), Austria (Laminger, 1973*b*), Belgium (Chardez, 1961*b*), British Isles (Cash & Hopkinson, 1909), Congo (Štěpánek, 1963), Czechoslovakia (Štěpánek, 1967), Germany (Schönborn, 1962*a* & *b*), Italy (Grandori & Grandori, 1934; Rampi, 1950), Java (Bartoš, 1963*a*), Netherlands (Hoogenraad & Groot, 1940), Roumania (Godeanu *et al.*, 1972), Spain (Gracia, 1972*b*), United States of America (Laminger *et al.*, 1979), West Africa (Decloitre, 1948).

Remarks. Penard's original description stated that the shell was–' pyriform, with or without narrowing of the mouth, chitinoid, slightly yellow, covered with small scales or particles of amorphous silica, plates, sufficiently transparent to examine the contents' and that specimens rarely exceeded 30 μm in length. Cash & Hopkinson (1909) described specimens between 65–70 μm in length that they tentatively identified as *D. pulex,* but on the basis of both Penard's and the present description it is now suggested they should be reassigned.

The description of *D. minuta minor* given by Godeanu (1972), shell colourless circular in cross section but with an irregular outline because of added quartz particles and a circular aperture, is so similar to that of *D. pulex* that it must be considered a synonym. The range of measurements given are also similar to those quoted here (see Table 1).

Although Penard gave 30 μm as the maximum length for this species, in the described sample two specimens were just in excess of 40 μm and two 30 μm, but in all other respects were similar to the smaller specimens, and all are considered to represent *D. pulex.*

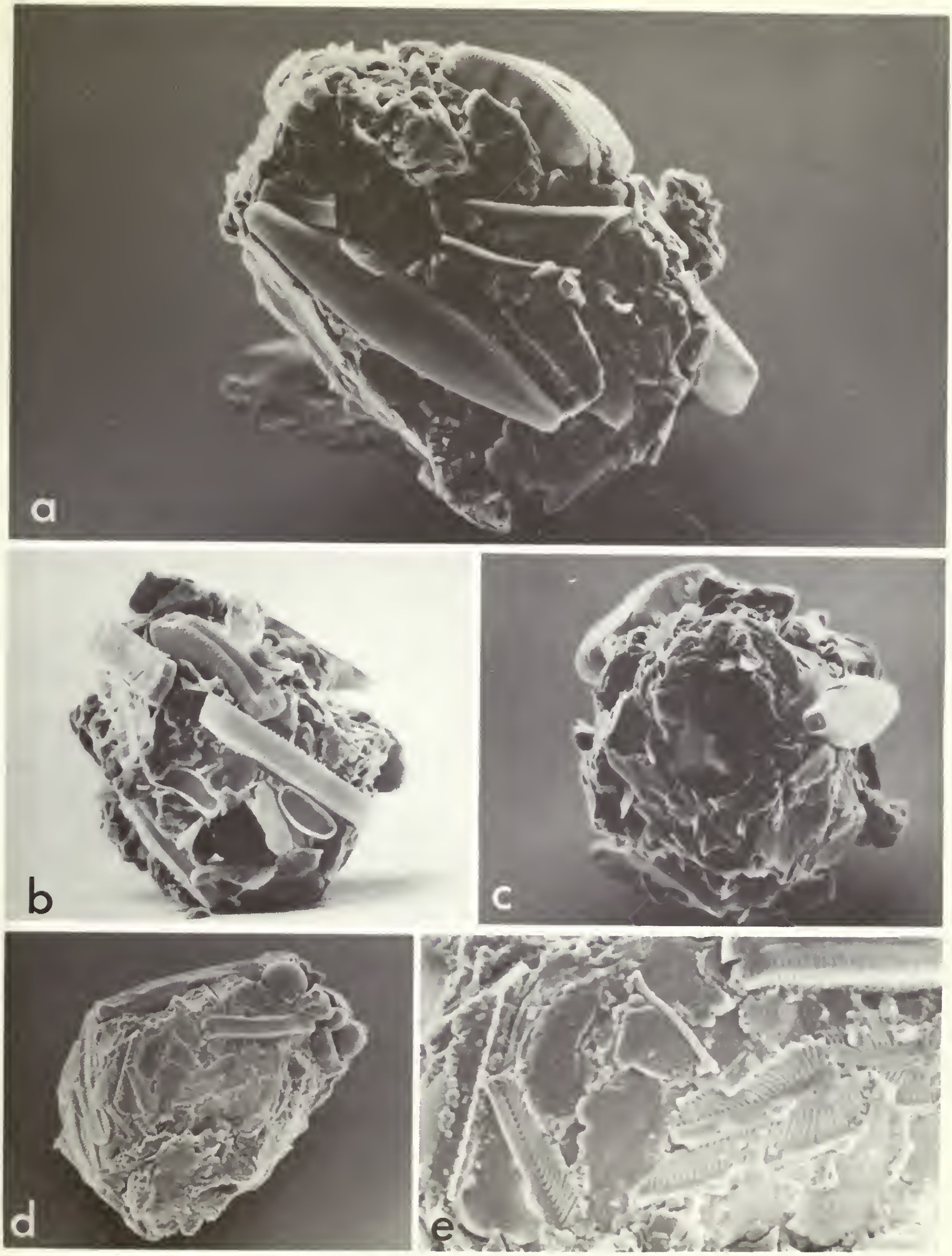

Fig. 14 *Difflugia pulex:* a, lateral view ×1800; b, apertural view of specimen with irregular apertural opening ×1300; c, apertural view of specimen (a.) with circular aperture ×1500; d, lateral view of specimen mainly made of flattish particles ×1600; e, shell surface showing mixture of flat components ×5100.

Difflugia tenuis (Penard, 1890) comb. nov.

Difflugia pyriformis var. *tenuis* Penard, 1890
Difflugia oblonga var. *tenuis* Wailes & Penard, 1911

DESCRIPTION. The shell is usually transparent, cylindrical or slightly pyriform, composed of a mixture of mainly small to medium pieces of angular quartz, but with an occasional large particle added (Figs. 15a & b). Sometimes additional particles give a pointed outline to the aboral region, instead of the usual rounded contours. Organic cement is seen frequently as single units between shell components (Fig. 15d), and occasionally in small patches where these units are in a network with a mesh diameter of 350–400 nm and walls 180–220 nm thick (Fig. 15e). The mesh surface is characterised by a thin, usually central, inner ring about 150–200 nm in diameter (Fig. 15e). The aperture is roughly circular, often having an irregular outline because of the mixture of particles surrounding it (Fig. 15b).

One specimen with projections similar to the rigid 'filament' structures described by Penard (1890), occurred in the present sample (Fig. 15c). These projections usually arise from a common base, on the surface of the quartz particles, and vary in size and number (Fig. 16a). The projections are about 250 nm in diameter and may be up to 7 µm in length, as many as fifteen have been seen sharing a common base (Fig. 16b). On the present evidence they seem to be rosettes of bacterial rods rather than the parasitic organisms suggested by Penard (1890).

MEASUREMENTS (in µm). See Tables 1 and 2.

MATERIAL EXAMINED. Specimens were collected from *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980 and Mynnd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

GEOGRAPHICAL DISTRIBUTION. Argentina (Dioni, 1970), British Isles (Cash *et al.*, 1919), Germany (Penard, 1890), Poland (Golemansky, 1970), Venezuela (Grospietsch, 1975).

REMARKS. Although the specimens described here are a little longer than those reported by Penard (1890) they are otherwise in good agreement with his description. This species has been identified previously on only a few occasions, but this may be due to its being mistaken for the more common species in this size range, for example *D. penardi* and *D. rubescens*. There remains the question of specific biological requirements, food, temperature, pH etc., which may be the reason why although the site at Holmsley has been sampled regularly for five or six years, March 1980 was the first time that this species has been seen there and then it appeared in significant numbers. This species is distinguished by its shape, size of aperture and the pattern of the organic cement.

Difflugia viscidula Penard, 1902

DESCRIPTION. This species has been redescribed recently by Ogden & Hedley (1980) but is reported again with some additional information.

The shell is opaque, pyriform or elongate ovoid, aborally it is usually rounded (Fig. 17a) but may occasionally be pointed. It is composed of a mixture of different sizes of angular quartz, with organic cement seen infrequently as part of the surface matrix. The cement appears as single units squashed together so that they are adjacent or overlap (Fig. 17c). The aperture is circular and usually surrounded by small particles which give it a characteristic well-defined outline (Fig. 17b). The illustrated aperture has a cyst plug, which although broken at one edge has in general a smooth surface, suggesting that it is mainly organic but reinforced by particles of quartz. About 10% of the examined specimens had an apertural cyst plug.

MEASUREMENTS (in µm). See Tables 1 and 2.

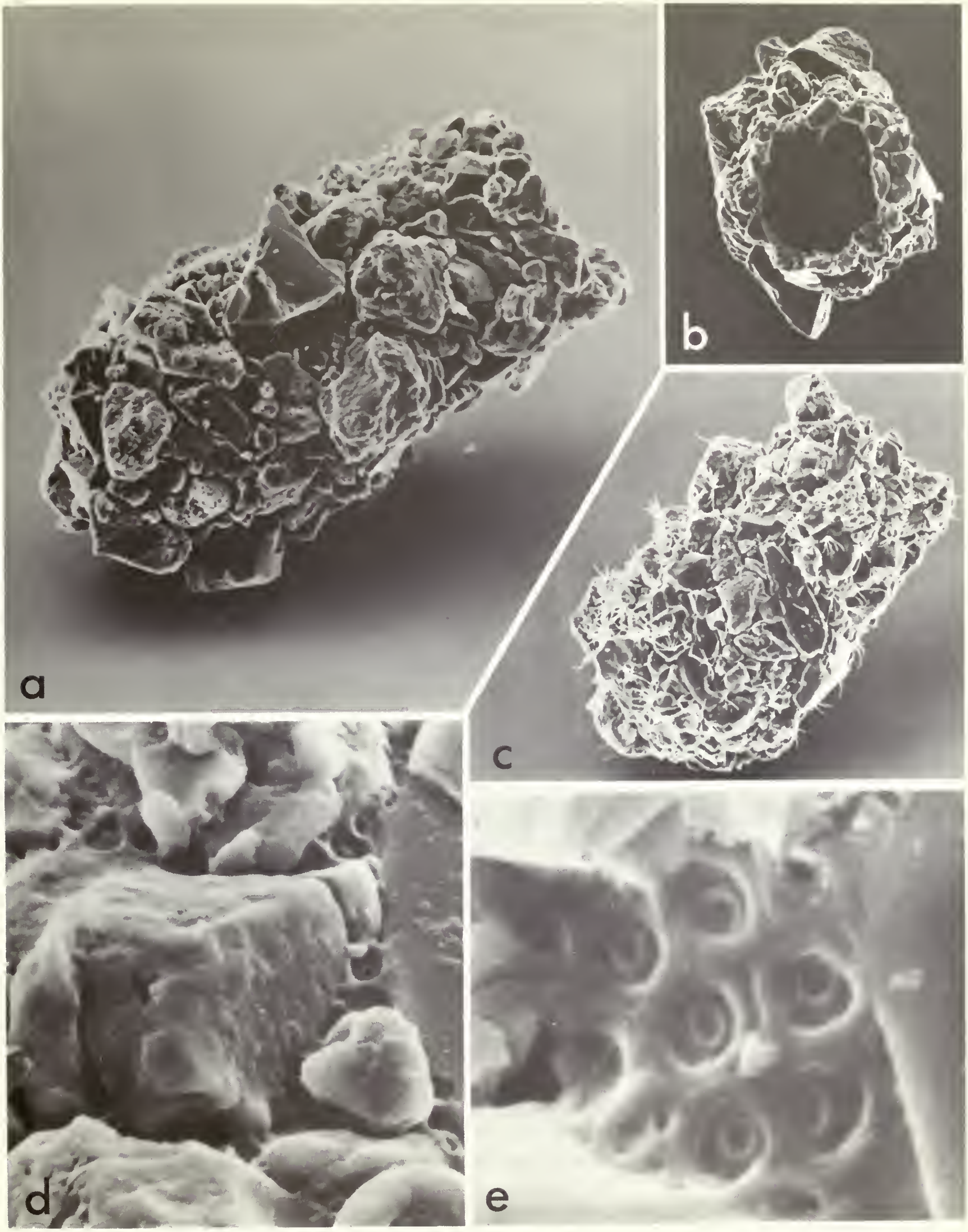

Fig. 15 *Difflugia tenuis:* a, lateral view ×1000, b, apertural view ×780; c, specimen with 'filament-like' structures projecting from the surface ×780; d, shell surface showing small areas of organic cement ×8100; e, detail of organic cement network ×24 000.

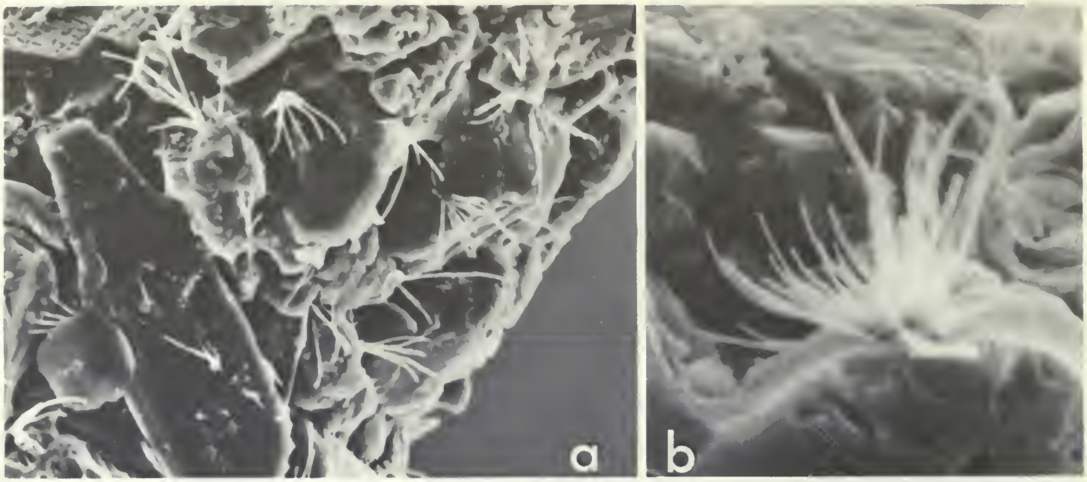

Fig. 16 *Difflugia tenuis:* a, portion of shell surface to show distribution of 'filament-like' structures ×2500; b, rosette of 'filaments', tentatively identified as bacterial rods ×7000.

MATERIAL EXAMINED· Specimens were collected from a sample of *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980.

GEOGRAPHICAL DISTRIBUTION. Argentina (Boltovskoy & Lena, 1974), Austria (Laminger, 1971), British Isles (Ogden & Hedley, 1980), Germany (Schönborn, 1962*a*, 1965, 1975), Java (Bartoš, 1963*a*), Roumania (Godeanu *et al.,* 1973), Switzerland (Penard, 1902).

REMARKS. The present material extends the measurements we gave previously (Ogden & Hedley, 1980) to encompass those given by Penard (1902). There remains the problem of priority of names for these specimens because Penard (1902) described two distinct species, namely *D. lemani* Blanc, 1892 and *D. viscidula* sp. nov., which he differentiated mainly on size; the former being 50–85 µm long (three individuals were 100–200 µm) and the latter 180–260 µm long. When he later found (Penard, 1905) that he had used incorrect measurements for *D. lemani* he suggested that *D. viscidula* should be regarded as a synonym. However, this proposal left his description of specimens under the name *D. lemani*–Penard, 1902 p. 249, without a proper designated name. They were divided into two series, the first slim, between 75–85 µm long and the second wider, but smaller about 50 µm long. It would appear that no subsequent report has rectified this situation, and it would seem that now is too late to change this because of the proliferation of species that have since been described and fall within the size range of the earlier description. Furthermore, it appears that Blanc's (1892) original description of *D. lemanii* might contravene Article 8 of the International Code of Zoological Nomenclature, because when first issued it would seem that it was not available by purchase or free distribution. There are no records of this publication in either this Museum's Libraries nor in the British Library, although I have recently obtained a photocopy from the Universitaire Lausanne. In Blanc's initial description of *D. lemanii* the shell dimensions varied as follows: body length between 180–310 µm, breadth 130–150 µm. and the aperture diameter was given as 110µm, it had a cylindrical body with almost parallel sides and the composition was such that it was friable and delicate. These measurements are in good agreement with Penard's 180–260 µm body length for *D. viscidula,* and those given here in Table 1 except for the diameter of the aperture, this latter feature is given as being equal to about half the breadth of the shell by Penard (1905). The diameter of the aperture and the pyriform rather than cylindrical shape of the body are considered sufficient to differentiate the present specimens and those of Penard (1902, 1905) from *D. lemanii* Blanc, 1892. This therefore leaves Penard's designated name of *D. viscidula* as valid and the specimens described here are so named.

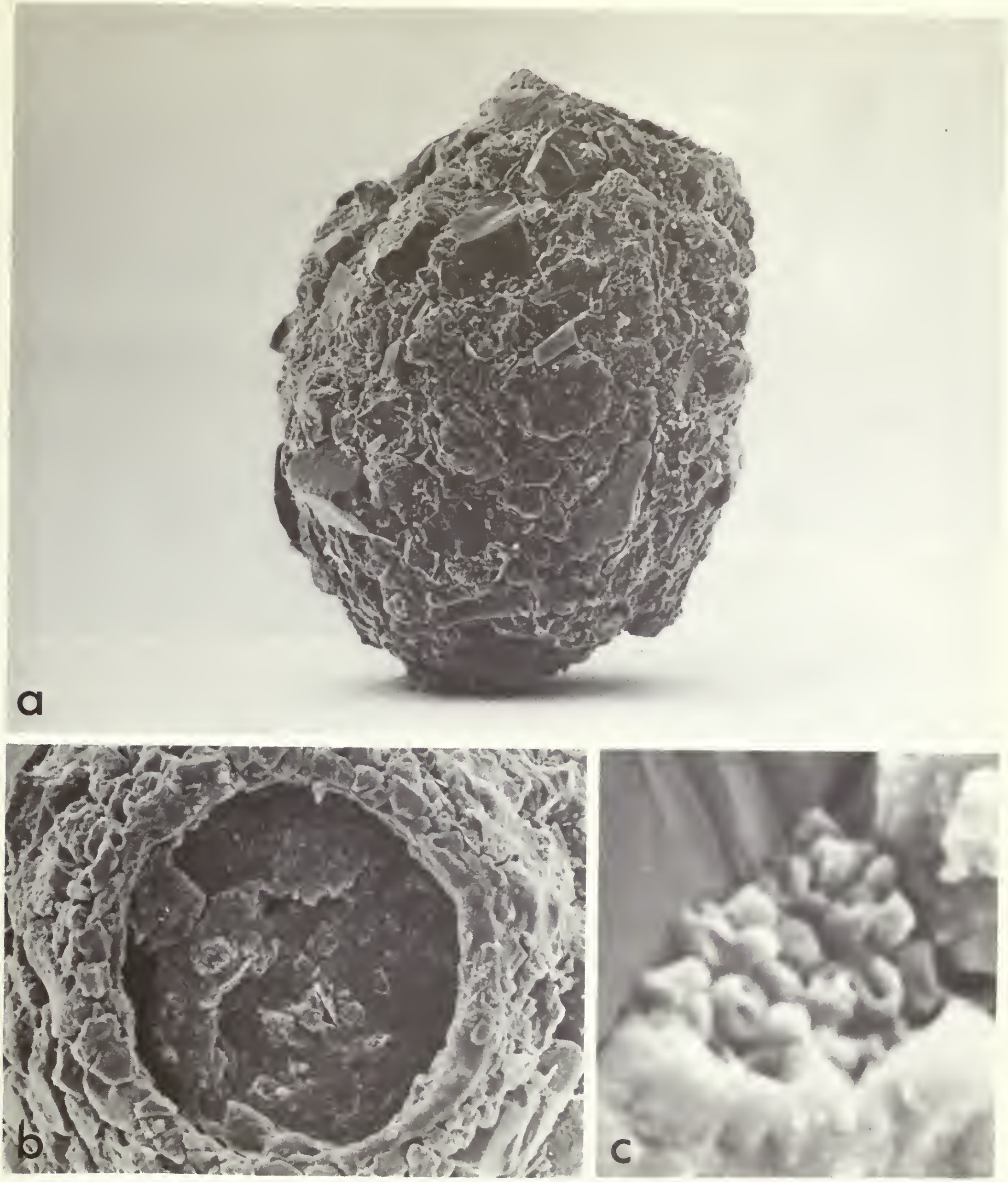

Fig. 17 *Difflugia viscidula:* a, lateral view ×410; b, detail of aperture which is blocked by a cyst plug ×1000; c, detail of organic cement ×13 000.

Pointed species or those with protruberances

Difflugia amphoralis Cash & Hopkinson, 1909

Description. The shell is transparent, squat pyriform with the aboral extremity tapering evenly to a point (Figs. 19a & b). It is composed mainly of medium pieces of quartz with small pieces mixed and so arranged to produce an intermediate smooth surface. Organic cement is seen in small patches between particles (Fig. 19d) and appears as rings fused to

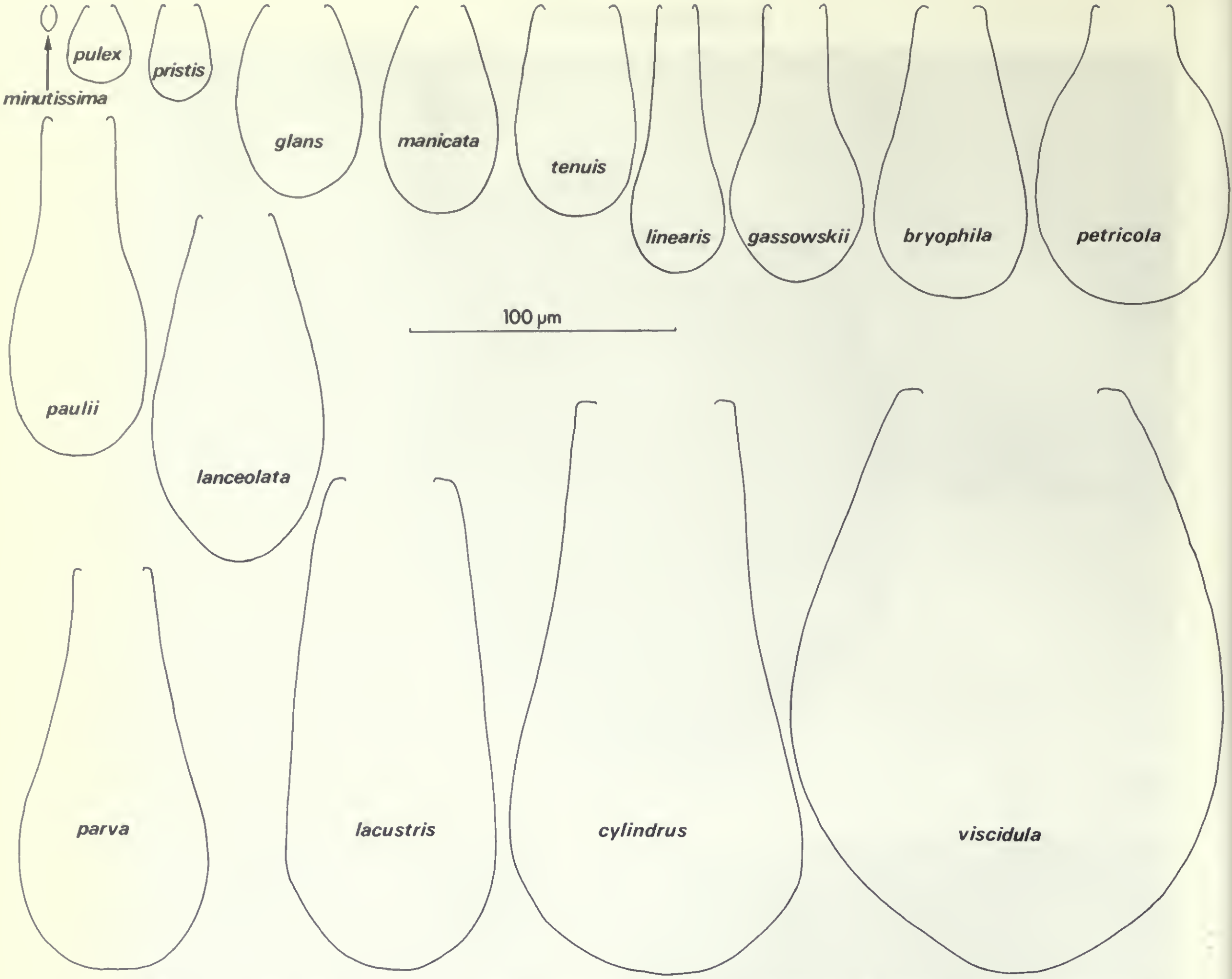
minutissima
pulex
pristis
glans
manicata
tenuis
linearis
gassowskii
bryophila
petricola
100 µm
paulii
lanceolata
parva
lacustris
cylindrus
viscidula

Fig. 18 Diagrams of pyriform and elongate species to illustrate the basic, outline based on measurements given in Table 2.

Table 2 Average dimensions of pyriform specimens listed in Table 1 and illustrated in Fig. 18.

Species	Length	Breadth	Diameter of aperture
D. minutissima	9	7	3
D. pulex	32	25	8
D. pristis	37	25	11
D. glans	71	46	20
D. manicata	77	47	16
D. tenuis	77	44	23
D. linearis	100	35	12
D. gassowskii	102	50	18
D. bryophila	108	58	19
D. petricola	111	72	25
D. paulii	126	50	21
D. lanceolata	128	64	25
D. parva	149	75	24
D. lacustris	183	78	34
D. cylindrus	211	112	45
D. viscidula	217	161	66

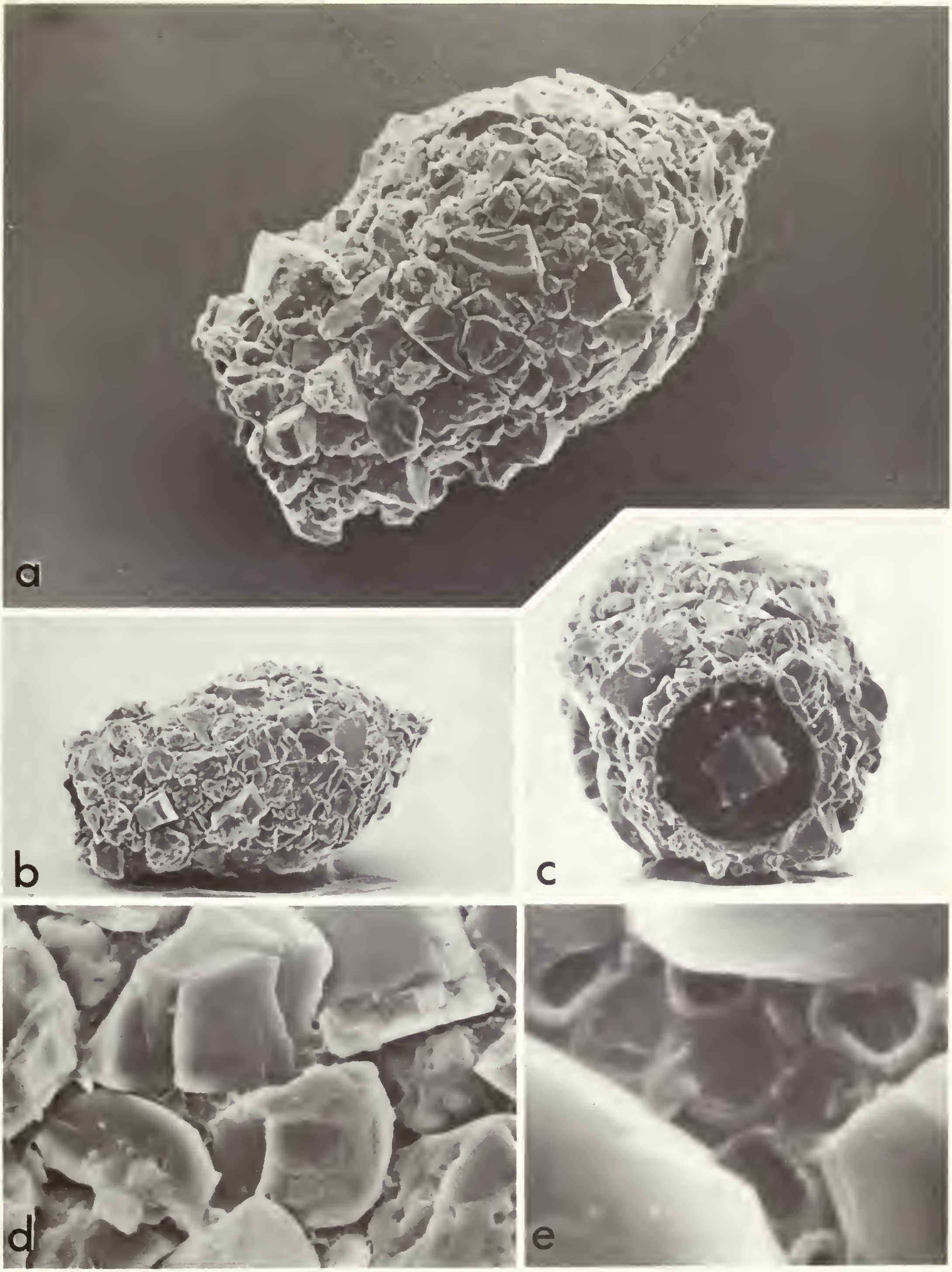

Fig. 19 *Difflugia amphoralis:* a, lateral view ×850; b, lateral view to show even aboral tapering ×500; c, apertural view ×760; d, shell surface showing areas of organic cement ×4500; e, detail of organic cement network ×24 000.

form a network, each mesh of which is about 380–450 nm internal diameter and the raised walls are 130 nm thick, a smooth membrane covers each enclosure (Fig. 19c). The circular aperture is surrounded by a small rim of mainly small particles to give a poorly defined border (Figs. 19a, b & c).

MEASUREMENTS (in µm). A single specimen: body length 109, breadth 62, diameter of aperture 28.

MATERIAL EXAMINED. The specimen was found in *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980.

GEOGRAPHICAL DISTRIBUTION. British Isles (Cash & Hopkinson, 1909), Tashkent (Pashintowa, 1929).

REMARKS. The structure of the shell in the present specimen differs from the original (Cash & Hopkinson, 1909) by being composed mainly of quartz particles, rather than 'amorphous (?siliceous) scales'. However, it should be noted that the specimens described by Leidy (1879) and quoted as synonyms of this species by Cash & Hopkinson (1909) are also composed mainly of 'quartz sand'.

Difflugia bicruris Gauthier-Lièvre & Thomas, 1958

DESCRIPTION. The shell is elongate ovoid, the sides being almost parallel with a slight tapering towards the aperture and the aboral extremity, the latter is rounded and has two small, equally spaced, protruberances or horns (Figs. 20a & c). It is composed of medium to large pieces of angular quartz, with some small particles being used in shaping the horns (Fig. 20d). The surface is rough but patches of organic cement are seen to form part of the shell matrix (Fig. 20e). Organic cement is arranged in the form of a regular network whose mesh has a diameter of about 300–350 nm and the distance between each enclosure is about 300 nm (Fig. 20f). The aperture is circular and surrounded by an even arrangement of small particles (Fig. 20b).

MEASUREMENTS (in µm). Two specimens: body length 202–207, breadth 95–115, diameter of aperture 41–58.

MATERIAL EXAMINED. Specimens were collected from aquatic plants taken at the banks of the River Brett, near Hadleigh, Suffolk, in August, 1979.

GEOGRAPHICAL DISTRIBUTION· Ivory Coast (Gauthier-Lièvre & Thomas, 1958), Poland (Golemansky, 1970).

REMARKS. Slight differences exist between the present specimens and those described by Gauthier-Lièvre & Thomas (1958). They have slightly larger general body measurements, although the proportions are directly comparable, and the horns are reduced in length, 20 µm here compared with 30–33 µm in the African specimens. Nevertheless, the descriptions are in good agreement showing that *D. bicruris* is distinctly ovoid with two aboral spines or horns.

Difflugia distenda nom. nov.

Difflugia acuminata var. *inflata* Penard, 1899

DESCRIPTION. The shell is transparent, pyriform with the aboral extremity acutely curved towards a small central tubular horn (Fig. 21a), although the extent of the angle may be less acute in a few specimens. It has an intermediate smooth surface and thickness, being composed mainly of small to medium pieces of quartz, with occasional diatom frustules added. Areas of organic cement are sometimes seen in the shell matrix as a network (Fig. 21c), with a mesh 350–400 nm in diameter and walls 150–200 nm thick (Fig. 21d). The

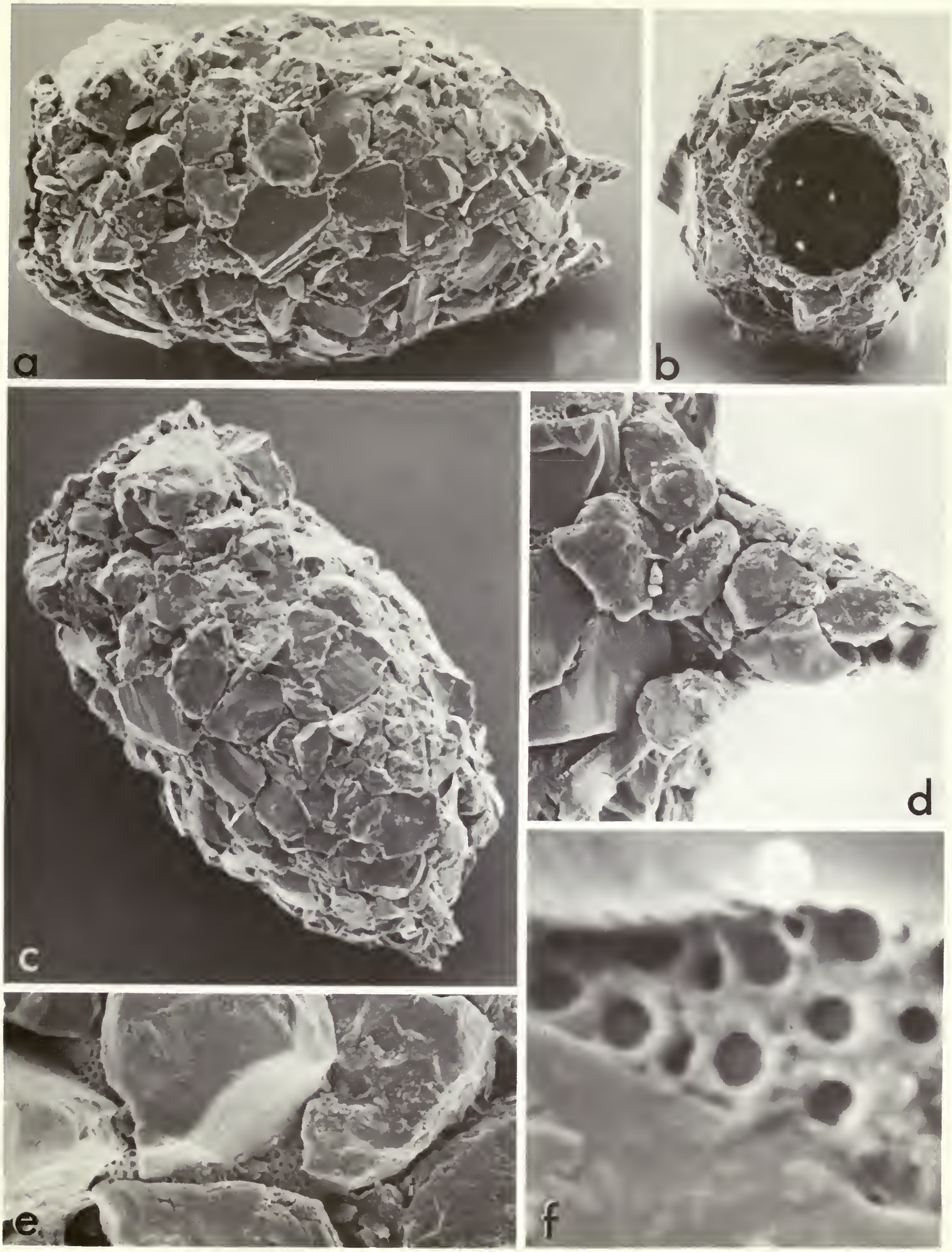

Fig. 20 *Difflugia bicruris:* a, lateral view illustrating the two aboral horns ×420; b, apertural view ×400; c, alternative lateral view with aboral horns not easily seen ×430; d, detail of aboral horn ×2500; e, portion of shell surface showing distribution of organic cement ×2700; f, detail of organic cement network ×25 000.

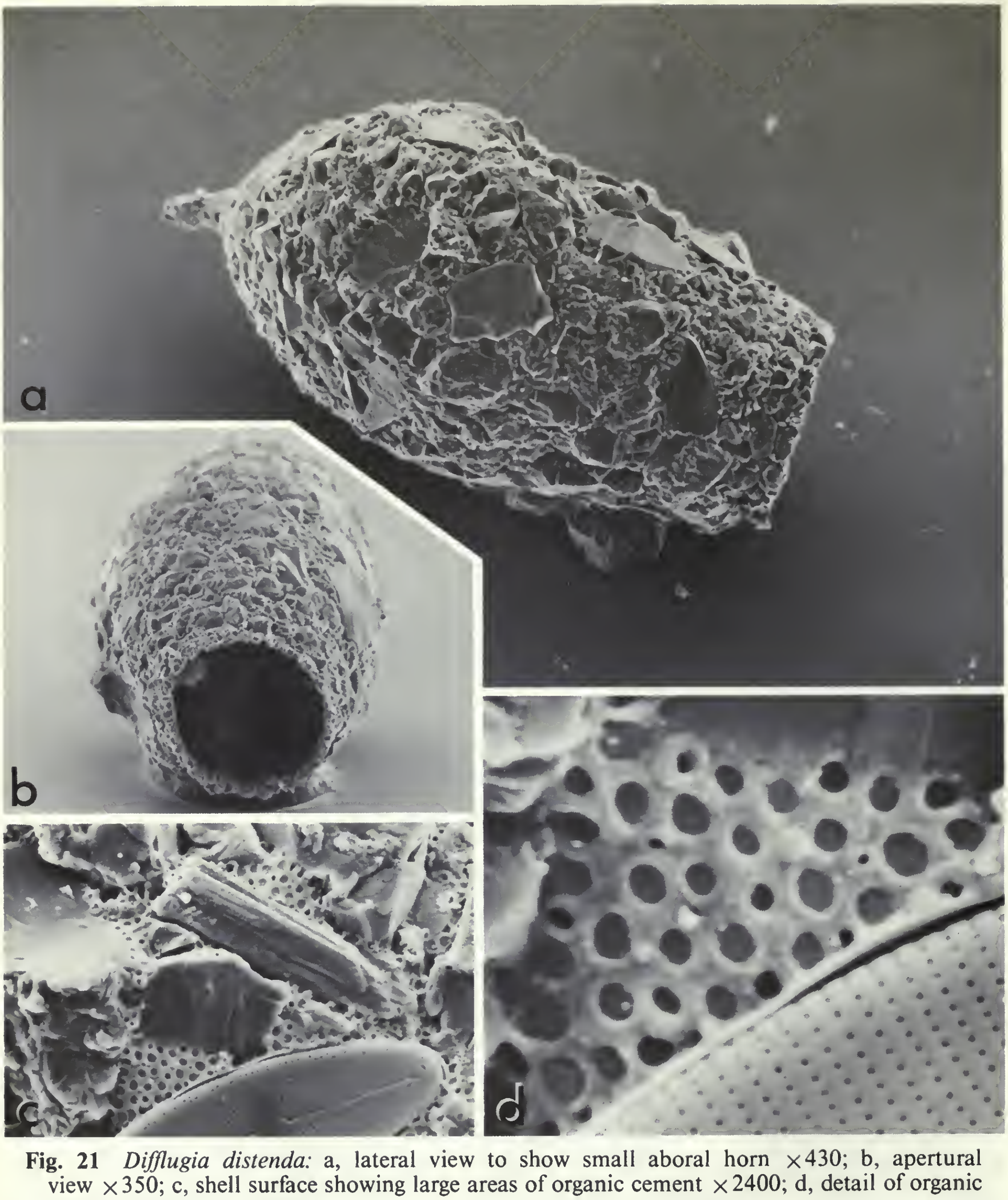

Fig. 21 *Difflugia distenda:* a, lateral view to show small aboral horn ×430; b, apertural view ×350; c, shell surface showing large areas of organic cement ×2400; d, detail of organic cement network ×11 000.

aperture is circular and usually surrounded by an even arrangement of small particles (Fig. 21b).

MEASUREMENTS (in µm). Based on ten specimens: body length 217–270, breadth 109–135, diameter of aperture, 58–64; B/L 0·53 ± 0·04, d/L 0·26 ± 0·02.

MATERIAL EXAMINED. Specimens were collected from a sample of *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980.

Geographical distribution. Algeria (Gauthier-Lièvre & Thomas, 1958), Austria (Laminger, 1971, 1973*b*), Belgium (Chardez, 1961*a*), British Isles (Cash & Hopkinson, 1909), Congo (Chardez, 1964; Gauthier-Lièvre & Thomas, 1958), France (Deflandre, 1962*b*; Thomas & Mabille, 1956), Gabon (Gauthier-Lièvre & Thomas, 1958), Ivory Coast (Gauthier-Lièvre & Thomas, 1958), Mexico (Laminger, 1973*b*), Morocco (Gauthier-Lièvre & Thomas, 1958), Poland (Golemansky, 1970; Moraczewski, 1965), Switzerland (Penard, 1902), Tashkent (Pashintowa, 1967).

Remarks. The variations of *D. acuminata*, and its twelve varieties has recently been illustrated by Chardez (1961). More recently it has been shown (Ogden, 1979) that *D. acuminata* Ehrenberg, 1838 has a distinctive elongate shape and an apparently unique organic cement pattern. Specimens described as var. *inflata* differ from this species in shape, size and organic cement pattern, the former is clearly demonstrated when the measurements are expressed as ratios, the comparable ratios for *D. acuminata* are B/L 0·36 ± 0·03 and d/L 0·15 ± 0·03 (Ogden, 1979).

The specimens described here agree well with Penard's (1899, 1902) original descriptions, and the differences from *D. acuminata* are considered sufficient to warrant specific designation. Our normal practise is to raise the variety name to specific rank, but on this occasion it is impracticable as the terminology *inflata* has been used several times in connection with specimens of *Difflugia,* for example *D. curvicaulis* var. *inflata* Decloitre, 1951.

Etymology· The specific name has been selected to reflect the inflated condition of the shell (L. *distenda* = swell out).

Difflugia labiosa Wailes, 1919

Difflugia amphora Leidy 1879 of Penard, 1901; 1902 & 1905

Description. The shell is opaque or dark brown, ovid or elongate ovoid, tapering from the mid-body region sharply to the rounded or pointed aboral extremity and more gradually towards the aperture (Fig. 22a). It is relatively thick and composed of quartz pieces so arranged that small particles fill the interstices between the larger pieces which form a mainly smooth surface (Fig. 22d). Organic cement is seen infrequently but is in the form of a network, each mesh being about 250–350 nm in diameter and is usually covered by a smooth membrane (Fig. 22e). The aperture is roughly circular but is sinuous with as many as six or seven undulations or lobes (Fig. 22b). It is slightly recessed into the main body, as though it was surrounded by a groove, the margin or lips, are thin and bordered by tiny particles of quartz. (Fig. 22b & c).

Measurements (in µm). Based on five specimens: body length 150–211, breadth 112–158, diameter of aperture 50–63.

Material examined. Specimens were collected from aquatic plants taken at the banks of the River Brett, near Hadleigh, Suffolk in August, 1979.

Geographical distribution. Austria (Laminger, 1971, 1975), Belgium (Chardez, 1980), British Isles (Cash *et al.,* 1919; Ogden & Hedley, 1980), Czechoslovakia (Ertl, 1965; Štěpánek, 1952, 1967), France (Thomas, 1954; Thomas & Mabille, 1956), Germany (Grospietsch, 1958; Schönborn, 1962*a,* & *b*), Netherlands (Hoogenraad & Groot, 1940), Poland (Moraczewski, 1961, 1965), Russia (Kourov, 1925), South Africa (Oye, 1931), Switzerland (Penard, 1902), Venezuela (Deflandre 1926*a*; Grospietsch, 1975).

Remarks. There has been some confusion over the correct name for this species, most recent authors using *D. amphora* Leidy, 1879, basing their identifications on the description given by Penard (1902). However, this name is preoccupied as it was used by Ehrenberg (1854, 1872) to describe a specimen which is no longer considered to be a species of *Difflugia.* It

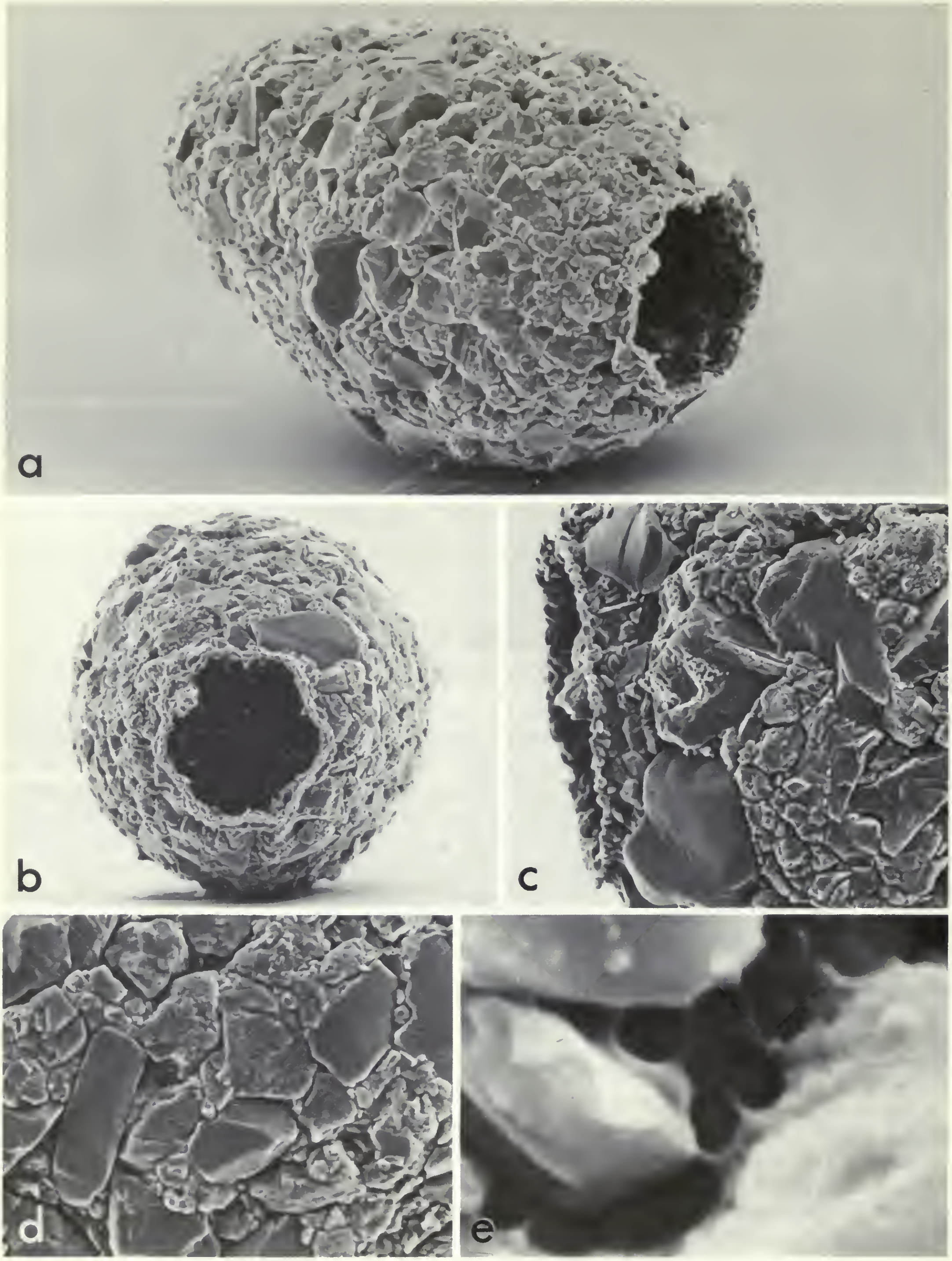

Fig. 22 *Difflugia labiosa:* a, latero-apertural view to show arrangement of particles ×580; b, apertural view illustrating the undulations or lobes ×470; c, lateral view of aperture to show slight groove and small particles on margin ×990; d, portion of shell surface showing the close packing of particles ×1300; e, detail of organic cement ×24 000.

follows that the later reports by Leidy (1874, 1879) default for the same reason. The latter report being more confusing by quoting *D. amphora* as a synonym of *D. urceolata*, whilst giving a figure of *D. ureceolata* var. *amphora*. Wailes (in Cash *et al.*, 1919) noted these earlier reports and proposed the new name *D. labiosa*, giving Penard's (1901, 1902, 1905) reports as synonyms. Earlier, Cash & Hopkinson (1909) had suggested that part of Leidy's (1879) description of *D. urceolata* var. *amphora* was a synonym of their new species *D. amphoralis*. The specimens described here are in good agreement with Penard (1902) who gave a range of body lengths 150–270 µm, but usually about 200–210 µm, and Wailes who suggested that it was a rare species from his single 265 µm long specimen.

This species is distinct in its ovoid-conical shape plus the lobed aperture with distinct margin and recessed base.

Difflugia mamillaris Penard, 1893

Description. The shell is colourless or hyaline, ovoid elongate, swollen or arched in the mid-region but tapering at both extremities, to give a rounded protruberance aborally and gradually near the aperture to give a slightly pronounced neck (Fig. 23a). Irregularities in general shape are not uncommon, for example one specimen although tapered did not have an aboral protruberance, whilst another (Fig. 23c) tapered markedly from the mid-body region. It is composed mainly of small to medium pieces of quartz so arranged that the larger particles tend to be in the mid-body region whilst the extremities have the smaller particles, overall it usually produces an intermediate thickness of a single layer and a relatively smooth outline. Organic cement occurs in small patches as a network, which has walls about 80–130 µm thick between each mesh but sometimes 230 µm thick at junctions. Each mesh is about 250nm in diameter and is covered by a smooth membrane which is distinct in having three or four small white spots on the surface of each enclosure (Figs. 23d & e). The aperture is circular, composed of small particles, and roughly finished so that the margin appears uneven or serrated (Fig. 23b).

Measurements (in µm). Based on twenty-three specimens: body length 93–111, breadth 54–72, diameter of aperture 23–31.

Material examined. Specimens were collected from a sample of aquatic plants taken at the banks of the River Brett, near Hadleigh, Suffolk in August, 1979.

Geographical distribution. Austria (Laminger, 1975), Congo (Chardez, 1964), Czechoslovakia (Štěpánek, 1967), Germany (Grospietsch, 1957), Switzerland, (Penard, 1901), Venezuela (Grospietsch, 1975).

Remarks. This species was initially described by Penard (1893) and redescribed in more detail by the same author (Penard, 1902). The present specimens are in good agreement with the latter description, including measurements which gave the body length as being generally between 90–110 µm with a few large specimens up to 130 µm long. More recently, Grospietch (1957) has shown a similar regularity in size of specimens from Lake Maggiore, giving length 90–113 µm and breadth 48–63 µm. Penard (1902) suggested that this species was rare in Swiss Lakes, and this appears to be the case in other localities judging by its reported incidence. Nevertheless, if the two recent reports (Grospietch, 1957 and the present) are used as indicators, it would appear that when present this species is usually abundant.

D. mamillaris is distinct in outline, even though the thin structure may be subject to distortion, and the unusual organic cement pattern.

Difflugia microclaviformis (Kourov, 1925) comb. nov.

Difflugia oblonga var. *microclaviformis* Kourov, 1925

Description. The shell is brown, pyriform with a distinct aboral protruberance (Fig. 24a). It

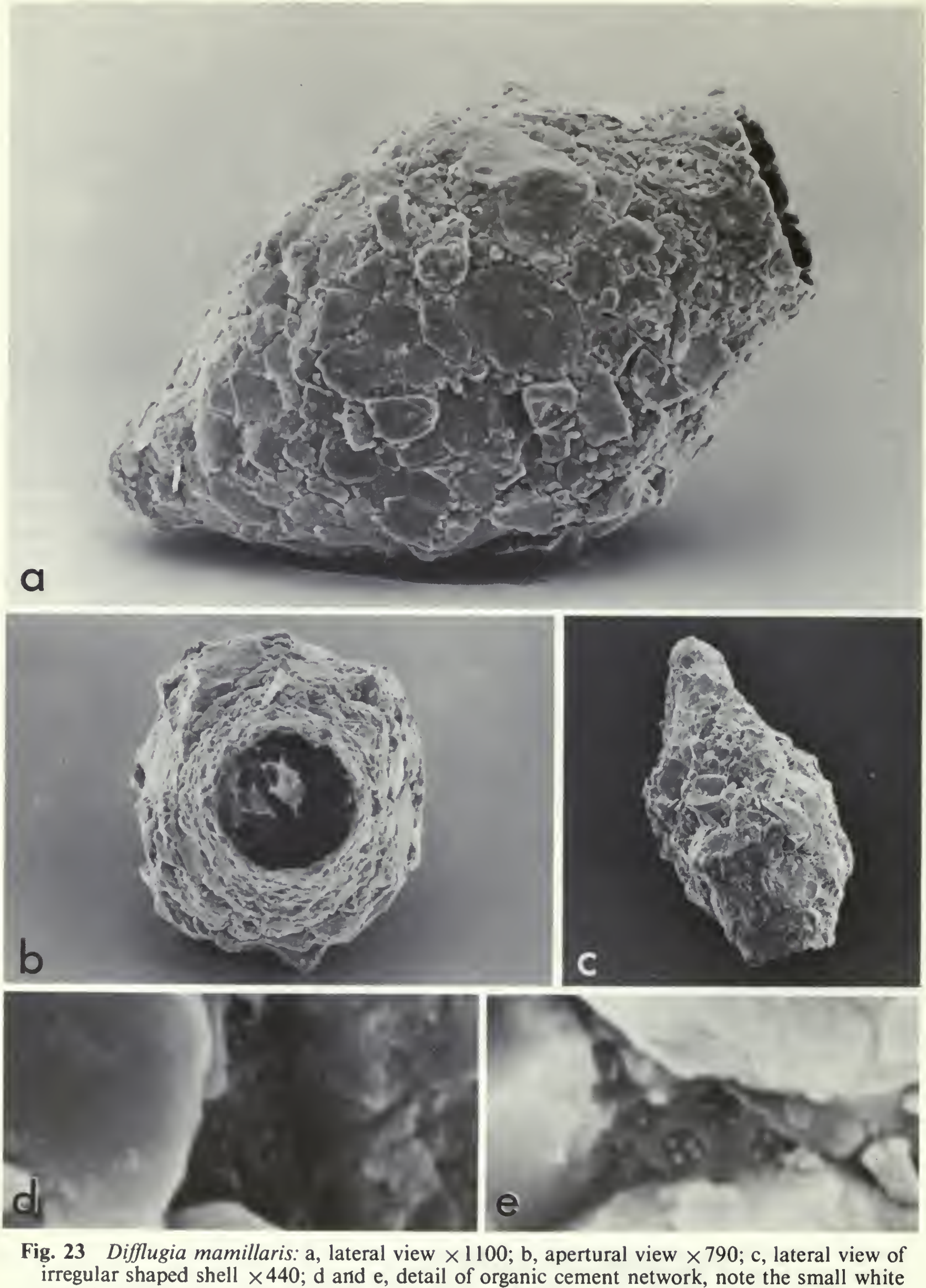

Fig. 23 *Difflugia mamillaris:* a, lateral view ×1100; b, apertural view ×790; c, lateral view of irregular shaped shell ×440; d and e, detail of organic cement network, note the small white spots in each enclosure which is a regular feature ×24 000.

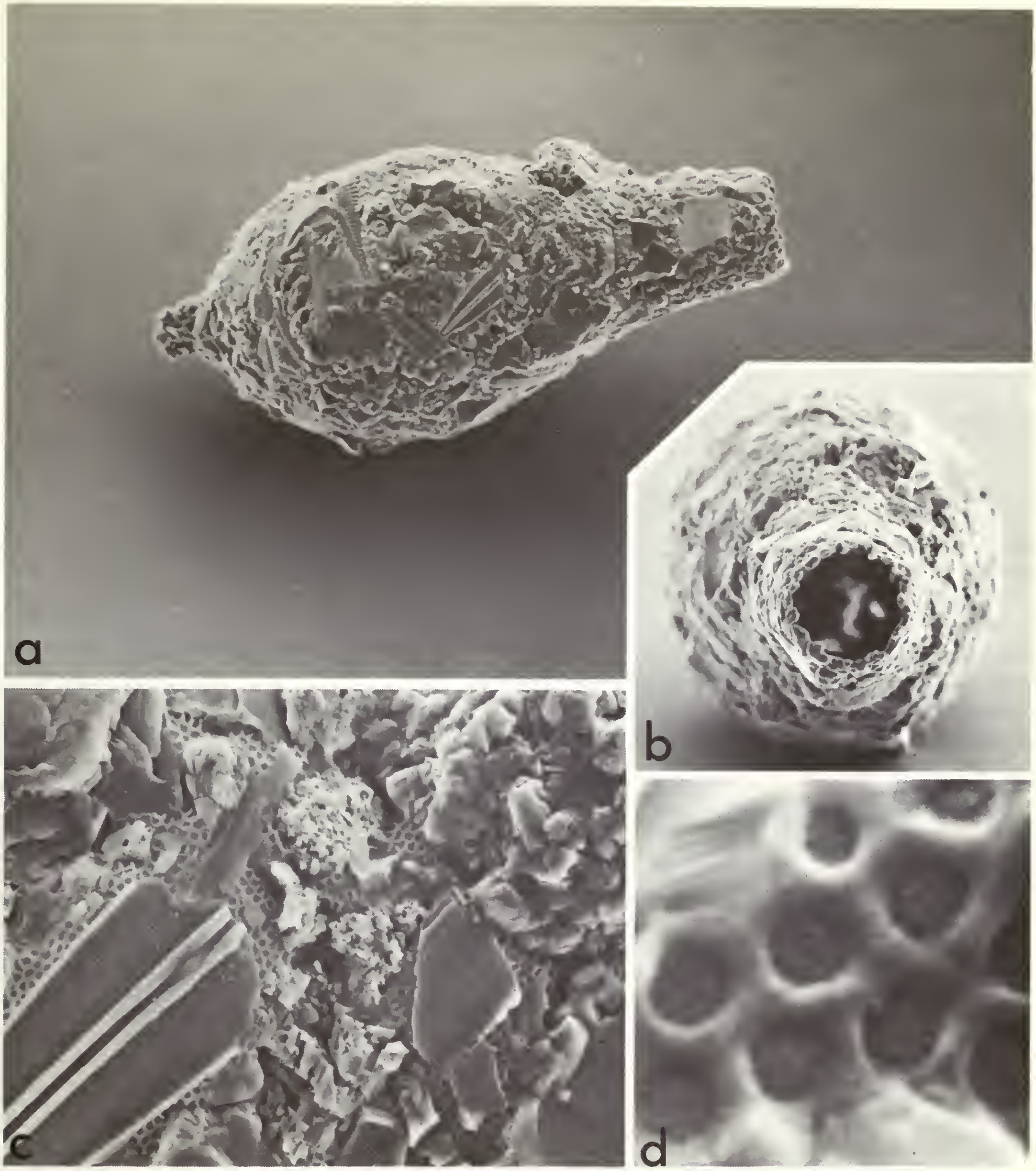

Fig. 24 *Difflugia microclaviformis:* a, lateral view ×230, b, apertural view ×530; c, shell surface illustrating the arrangement of particles and organic cement ×2600; d, detail of organic cement network, note the regular distribution of small pores in each enclosure ×33 000.

is composed of small to medium pieces of quartz, some flattish diatom frustules, and a network of organic cement is often seen as part of the shell matrix (Fig. 24c). The result is a smooth surface and a well defined outline. The mesh of the organic cement has a diameter of 300 nm with walls 150 nm thick, and a smaller network, with pores about 30 nm in diameter, covers each mesh enclosure (Fig. 24d). The aperture is circular and surrounded by small particles (Fig. 24b).

Measurements (in µm). Based on two specimens: body length 202–206, breadth 88–89, diameter of aperture 27–28.

Material examined. Specimens were collected from a sample of *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire, in March, 1980.

Geographical distribution. Algeria (Gauthier-Lièvre & Thomas, 1958), Argentina (Vucetich, 1978), Austria (Laminger, 1973*b*), Congo (Gauthier-Lièvre & Thomas, 1958), France (Thomas, 1954), Ivory Coast (Gauthier-Lièvre & Thomas, 1958), Mexico (Laminger, 1973*a*), Roumania (Godeanu *et al.*, 1973), Russia (Kourov, 1925), Spain (Gracia, 1972*a*).

Remarks. This species when initially described (Kourov, 1925) had a body length not greater than 185 µm, whereas Gauthier-Lièvre & Thomas, 1958 gave dimensions similar to those given here. It is redescribed to show its marked similarity to *D. claviformis*, lack of material prevents a complete comparison and the identification must be treated as tentative. *D. microclaviformis* appears to differ from *D. claviformis* (see Ogden, 1979) in size and possibly the organic cement pattern.

Difflugia molesta Penard, 1902

Description. The shell is brown, ovoid or ovoid-elongate, sometimes with a small apertural collar and arched aborally (Fig. 25a). It is composed of a mixture of quartz particles and diatom frustules, the former usually being predominant. Organic cement is seen as a network between particles, either as part of the shell matrix or occasionally at junctions. The rings that form the network are about 650–750 nm internal diameter with the dividing wall being 100–150 nm thick, a second thin, inner wall lies close to the main wall and in the illustrated specimen the covering membrane is either holed or figured (Fig. 25c). The aperture is roughly circular, irregular in outline, and mainly surrounded by small particles (Fig. 25b).

Measurements (in µm). Based on four specimens: body length 106–114, breadth 61–87, diameter of aperture 28–43.

Material examined. Specimens were collected from *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980 and Mynnd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

Geographical distribution. Roumania (Godeanu *et al.*, 1973), Russia (Kourov, 1925), Switzerland (Penard, 1902).

Remarks. These specimens are tentatively identified here as *D. molesta,* the query arising due to their similarity with *D. amphoralis*. Of the four specimens examined, the smallest (Fig. 25a) bears the closest resemblance being slim, with a small aperture and differing in the absence of a pointed aboral protruberance. The three broader specimens have a wider aperture, a narrow neck and are arched aborally. In addition, there are differences in the organic cement patterns between the two species, but altogether there is insufficient information to satisfactorily resolve the problem.

Difflugia tricornis (Jung, 1936) comb. nov.

Difflugia elegans forma *tricornis* Jung, 1936

Description. The shell is pyriform, with a slight broadening near the aperture, and is characterised by three, evenly spaced, aboral spines (Fig. 26a). The surface is rough and mainly composed of a mixture of medium and large pieces of angular quartz, the spines have medium particles at their wide bases but small particles are used progressively as they taper to a point. Small areas of organic cement are seen between the particles (Fig. 26c), usually in the form of a regular network (Fig. 26d), having a mesh between 350–400 nm internal

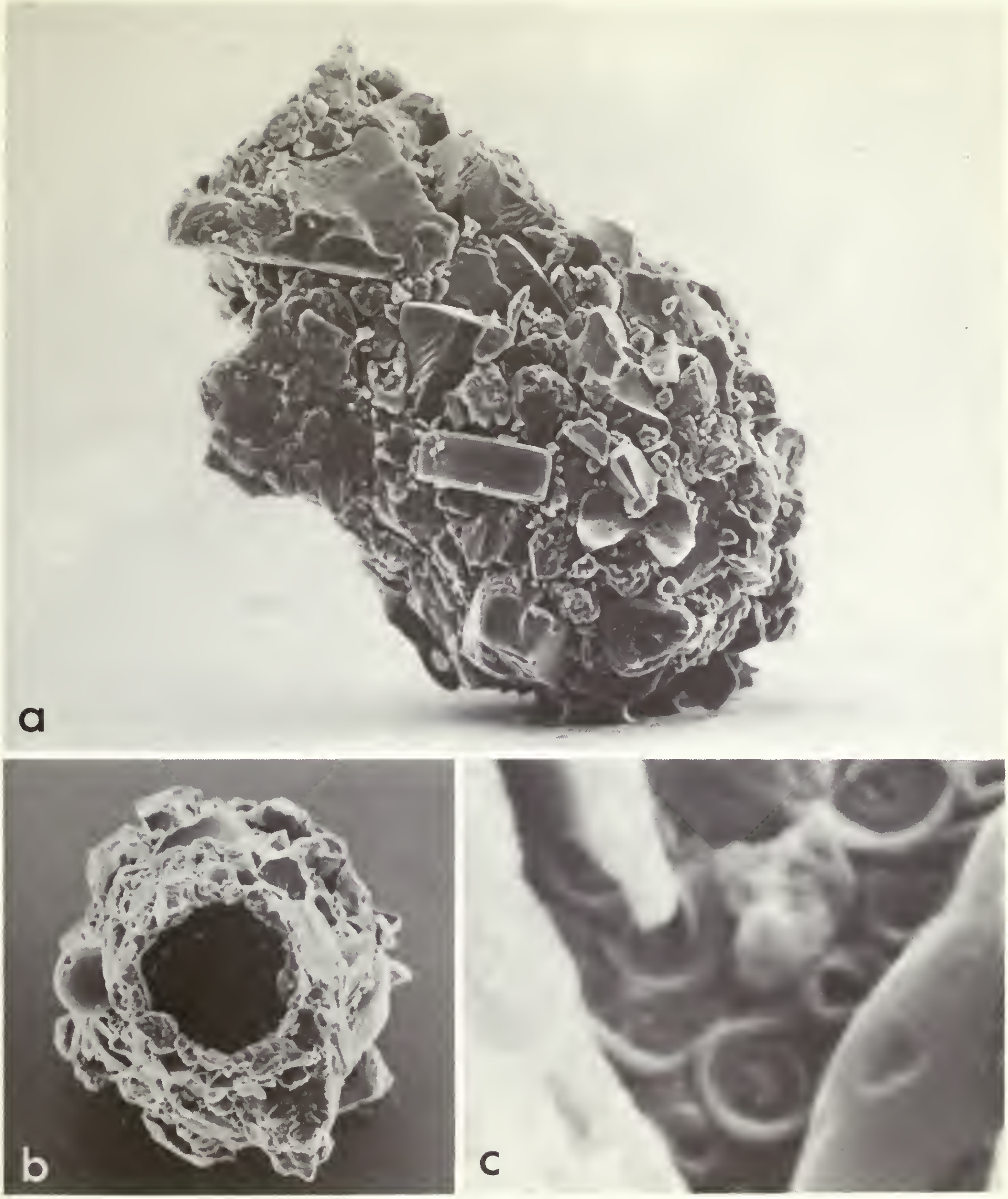

Fig. 25 *Difflugia molesta:* a, lateral view ×910; b, apertural view ×740; c, detail of organic cement to show arrangement of rings and figured centre ×24 000.

diameter and dividing walls about 150 nm thick although at some junctions there are larger areas. The aperture is circular and surrounded by an irregular assortment of particles (Fig. 26b).

Measurements (in µm). One specimen: body length 116, breadth 82, diameter of aperture 40.

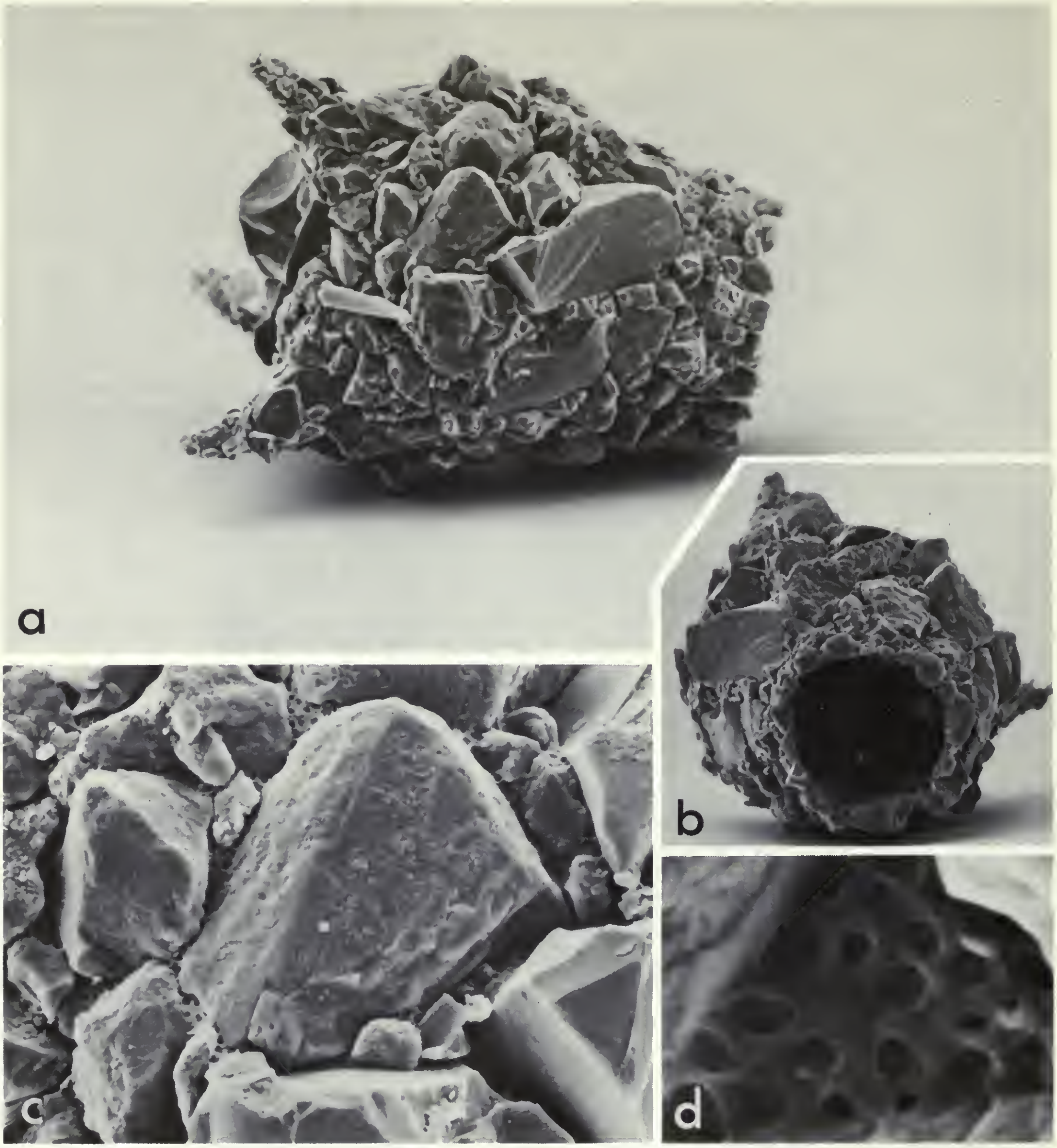

Fig. 26 *Difflugia tricornis:* a, lateral view to show the three equally spaced aboral spines ×690; b, apertural view ×530; c, portion of shell surface showing small areas of organic cement ×2300; d, detail of organic cement network ×14 000.

Material examined. The specimen was collected from aquatic plants taken at the banks of the River Brett, near Hadleigh, Suffolk in August, 1979.

Geographical distribution. Germany (Jung, 1936), Sudan (Gauthier-Lièvre & Thomas, 1958).

Remarks. In the earlier descriptions (Jung, 1936; Gauthier-Lièvre & Thomas, 1958) the specimens resembled *D. elegans* except for the three aboral spines which were stated to be randomly placed, although Jung (1936) cited Penard's figures referring to much smaller animals. Differences in the shape and structure of *D. elegans* examined recently by the author (Ogden, 1979; Ogden & Hedley, 1980) have been confined to the size and structure of the single aboral spine or horn, whilst the body length was usually of a standard size 110–160 µm.

The present specimen has three, equally spaced, aboral spines and the body breadth is markedly wider, features that are considered sufficiently different from *D. elegans* to warrant a specific designation. The earlier reports are placed, with reservations, in synonymy.

Difflugia ventricosa Deflandre, 1926

Description. The shell is colourless, elongate, with a slight swelling in the aboral half of the body which then tapers to a sharp point (Fig. 27a). It is composed of a mixture of quartz, diatom frustules and flagellate cysts to give a thin, irregular surface. Organic cement is frequently seen between particles in the form of a network (Fig. 27c), made of rings about 600–680 nm in diameter with walls 180–250 nm thick (Fig. 27d). In some instances the rings are fused and appear to have lost or merged their walls (Fig. 27e). The aperture is circular and usually surrounded by small particles (Fig. 27b).

Measurements (in µm). Two specimens: body length 177–199, breadth 64–66, diameter of aperture 30–31.

Material examined. The specimens were collected from a sample of *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980.

Geographical distribution. Belgium (Chardez, 1973), Congo (Gauthier-Lièvre & Thomas, 1958), France (Thomas & Mabille, 1956), Ivory Coast (Gauthier-Lièvre & Thomas, 1958), Venezuela (Deflandre, 1926*a*).

Remarks. A redescription of *D. ventricosa* has recently been given by Chardez (1973) who compared it with other species having a pointed aboral extremity. It is interesting to note that he made no comparison with *D. venusta*, although from the description given here (below) there would seem to be some similarities. The tabulated measurements given by Chardez (1973) from earlier descriptions, are in good agreement with the exception of those given by Thomas & Mabille (1956).

This species is distinct in having a thin, elongate outline which is sharply pointed aborally.

Difflugia venusta (Penard, 1902) comb. nov.

Difflugia pyriformis var. *venusta* Penard, 1902
Difflugia oblonga var. *venusta* (Penard, 1902) Cash & Hopkinson, 1909

Description. The shell is pale yellow or hyaline, cylindrical, gradually swelling from the aperture for about two-thirds of the body length to the broadest diameter and then tapering sharply in the last third to the bluntly pointed apex (Fig. 28a & b). It is composed mainly of small to medium pieces of quartz and diatom frustules arranged to give a relatively regular, intermediate smooth, outline apart from the occasional addition of a larger angular piece of quartz or diatom frustule. Small areas of organic cement are sometimes visible as a thick walled network with a covered mesh (Fig. 28d), but more often as thick walled rings about 450–600 nm in diameter and walls 150–220 nm (Fig. 28c). The aperture is usually circular and surrounded by small particles that give it an irregular margin (Fig. 28c).

Measurements (in µm). Based on three specimens: body length 174–188, breadth 68–76, diameter of aperture 30–32.

Material examined. Specimens were collected from a sample of *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in March, 1980.

Geographical distribution. Argentina (Dioni, 1970), Belgium (Chardez & Gaspar, 1976),

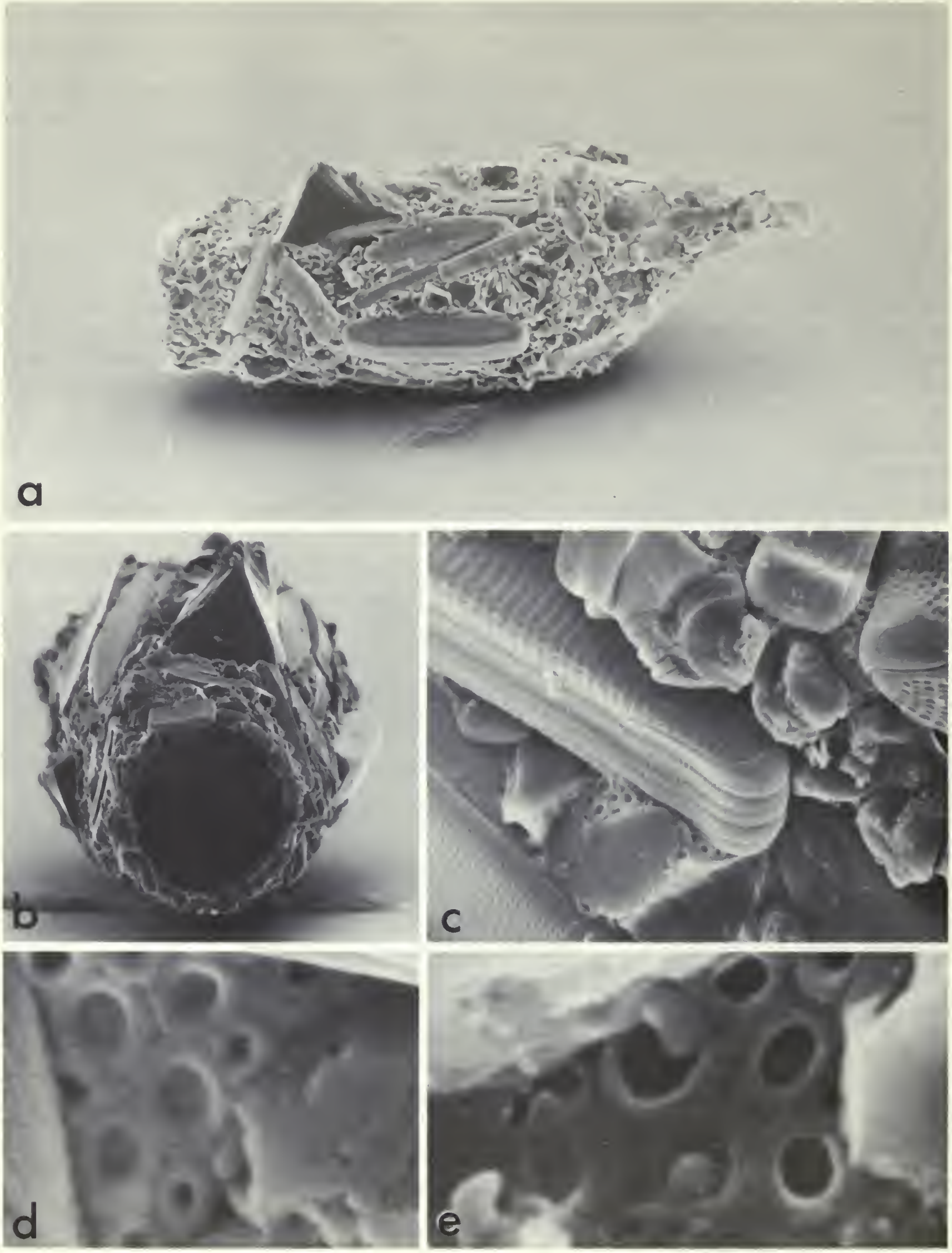

Fig. 27 *Difflugia ventricosa:* a, lateral view to illustrate tapering of aboral spine ×520; b, apertural view ×760; c, shell surface showing small areas of organic cement ×4700; d, detail of organic cement network of rings ×24 000; e, organic cement network with fused rings ×28 000.

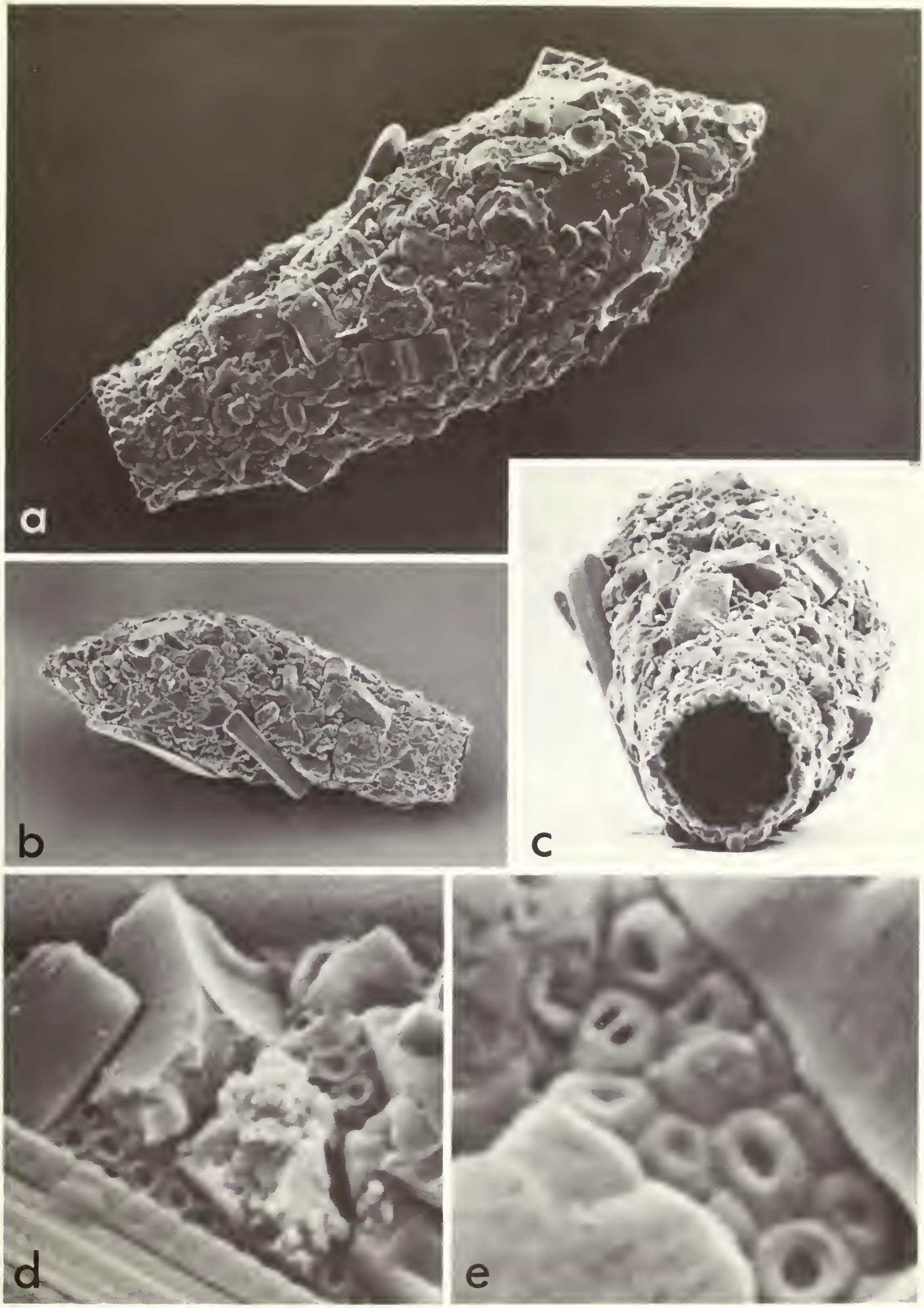

Fig. 28 *Difflugia venusta:* a and b, lateral views to show sharp tapering of aboral region ×570 and ×340; c, apertural view ×590; d, shell surface showing distribution of organic cement ×9200; e, detail of organic cement network ×24 000.

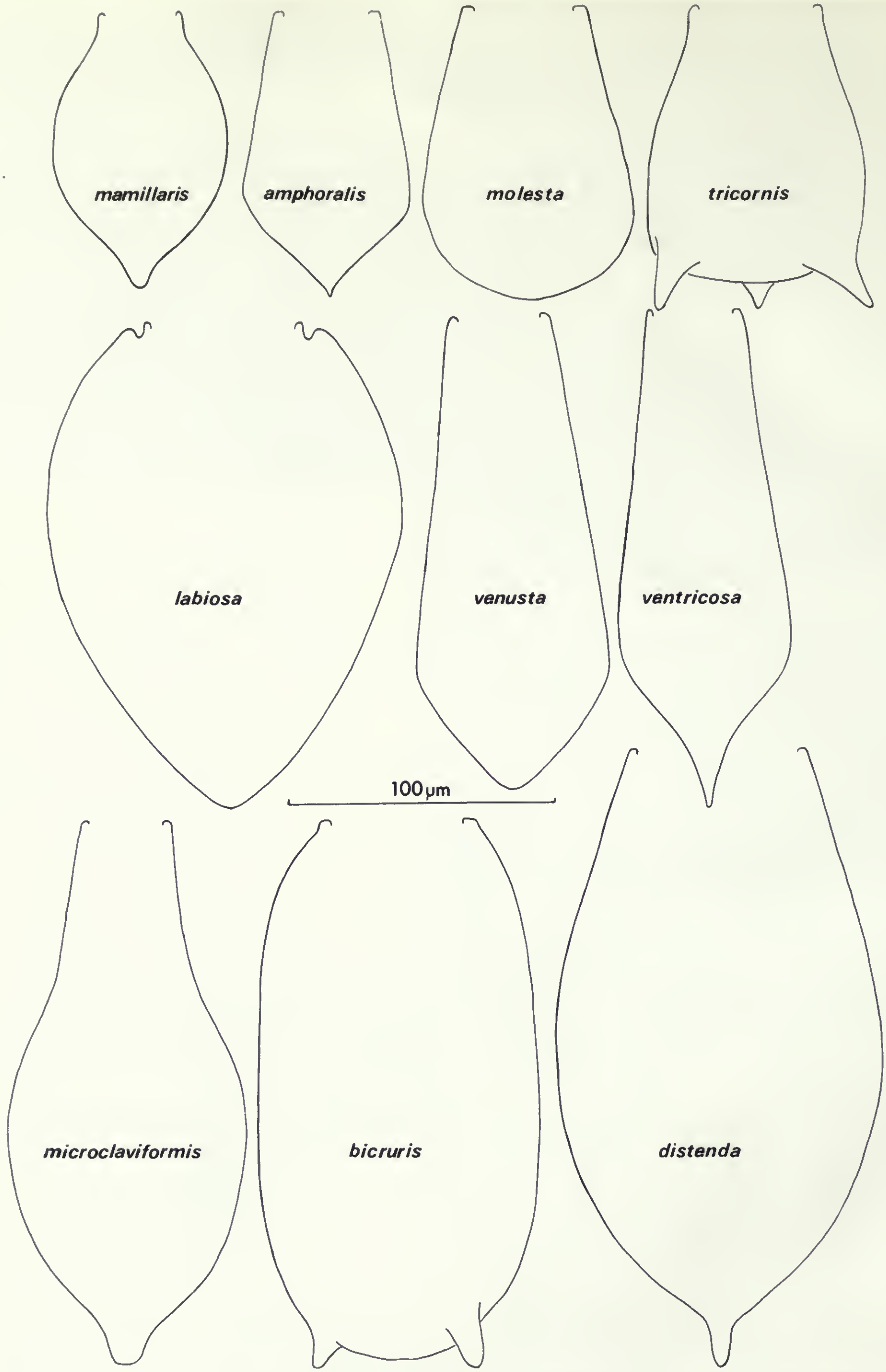
mamillaris
amphoralis
molesta
tricornis
labiosa
venusta
ventricosa
100 µm
microclaviformis
bicruris
distenda

Fig. 29 Diagrams of pointed species or those with protruberances to illustrate the basic outline, based on measurements given in Table 3.

Table 3 Average dimensions of pointed species or those with protruberances used to give basic outlines illustrated in Fig. 29

Species	Length	Breadth	Diameter of aperture
D. mamillaris	103	65	27
D. amphoralis	109	62	32
D. molesta	110	73	37
D. tricornis	116	82	40
D. labiosa	183	132	55
D. venusta	179	71	31
D. ventricosa	188	65	30
D. microclaviformis	204	88	27
D. bicruris	205	106	50
D. distenda	230	122	60

France (Thomas, 1954), Haute Volta, W. Africa (Gauthier-Lièvre & Thomas, 1958), Switzerland (Penard, 1902).

REMARKS. The present specimens agree well with the descriptions given by Penard (1902), Cash & Hopkinson (1909) and Gauthier-Lièvre & Thomas (1958) who considered it a variety of *D. pyriformis/oblonga,* although the shells described by Cash & Hopkinson (1909) were slimmer than those reported here and by Gauthier-Lièvre & Thomas (1958).

This species is distinct in the graceful outline with bluntly pointed aboral extremity and shell structure.

Ovoid or spherical species

Difflugia ampullula Playfair, 1918

DESCRIPTION. The shell is hyaline, ovoid and circular in cross section (Fig. 30a). It has a medium thickness and is composed mainly of small to medium pieces of quartz, arranged to give a clean outline with a smooth surface. Small areas of organic cement in the form of a network, are often seen as part of the shell structure (Fig. 30d). The mesh of the network is small about 300–350 nm in diameter with thin walls 50–100 nm thick, and an even smaller distinctive network covering each mesh enclosure (Figs. 30e & f). The aperture is circular, surrounded by a slightly raised collar of small particles, and the edge of the collar is often irregular (Figs. 30b & c).

MEASUREMENTS (in µm). Range of 39 specimens: body length 54–95, breadth 35–72, diameter of aperture 16–29.

MATERIAL EXAMINED. Specimens were collected from aquatic plants taken at the banks of the River Brett, near Hadleigh, Suffolk in August, 1979.

GEOGRAPHICAL DISTRIBUTION. Australia (Playfair, 1918).

REMARKS. The specimens described here differ slightly from the original description (Playfair, 1918) in the absence of a 'minute, pointed apiculate process' on the aboral extremity. However, this process was reported as being present sometimes, and as there is otherwise good agreement between the two reports, the specimens are designated as *D. ampullula*.

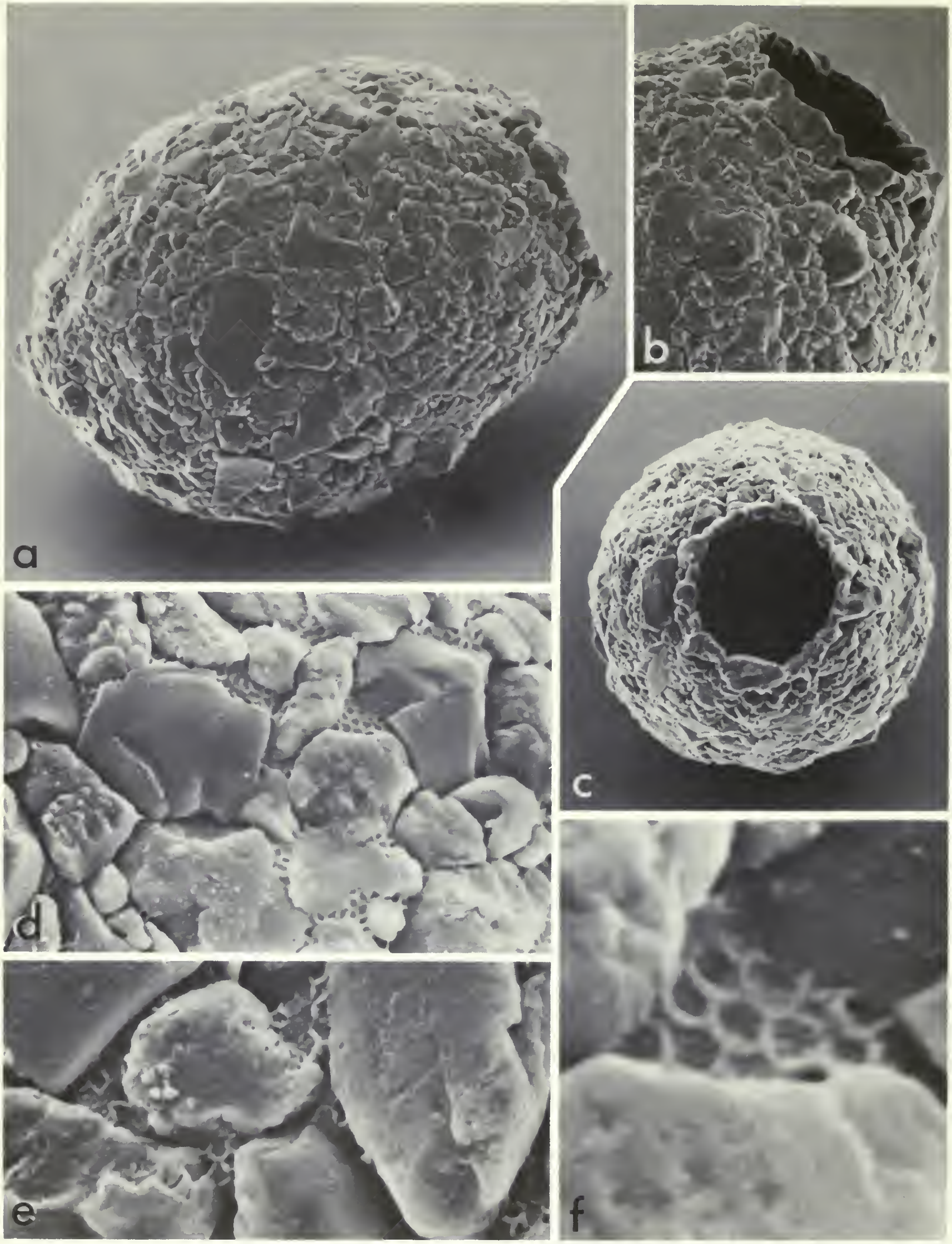

Fig. 30 *Difflugia ampullula:* a, lateral view ×1000; b, latero-apertural view of aperture to illustrate the small collar ×1200; c, apertural view ×770; d, portion of shell surface to show the arrangement of particles and organic cement ×5000; e, detail of shell surface ×7700; f, small area of organic cement network, note that each enclosure has an inner network ×25 000.

Difflugia angulostoma Gauthier-Lièvre & Thomas, 1958

Description. The shell is transparent, spherical and composed mainly of diatom frustules (Fig. 31a & b). The particles are packed close together with many overlapping, to give a rough surface. Organic cement is seen infrequently as small strands between particles (Fig. 31c). The aperture is usually circular (Fig. 31a), but it may have irregularities depending on the arrangement of surrounding diatom frustules.

Two groups of specimens with identical shell features but differing dimensions were examined, the 'a' specimens are from all four listed localities and 'b' specimens are from Three Shires Stone only.

Measurements (in µm)

	body length	breadth	diameter of aperture	B/L	d/L
8 specimens 'a'	40–56	40–48	18–23	0·94±0·06	0·42±0·06
8 specimens 'b'	60–82	50–73	28–51	0·87±0·09	0·56±0·05

Material examined. Specimens were collected from samples of *Sphagnum* moss gathered at four localities: Cranes Moor in May, 1977, Holmsley in May, 1978 both in the New Forest, Hampshire; Three Shires Stone, Wrynose Pass and Lanthwaite, both in Cumbria, June, 1979.

Geographical distribution. Algeria (Gauthier-Lièvre & Thomas, 1958), Argentina (Vucetich, 1973*a* & *b*), Congo (Gauthier-Lièvre & Thomas, 1958).

Remarks. This species was described by Gauthier-Lièvre & Thomas (1958), from specimens found in Algeria, who considered that it differed from *D. minuta* by the large size of the aperture, quoted as being about one-third of the breadth in diameter, and the covering diatoms. Both sets of the present specimens, 'a' and 'b', agree well with this description, having a large aperture about half the breadth diameter and are composed of diatoms. The 'b' specimens share almost similar dimensions to *D. angulostoma,* the latter having a body length 60–95 µm and aperture 30–45 µm, whereas the 'a' specimens are generally smaller. The difference in size between specimens 'a' and 'b' is more apparent when the ratios d/L are compared, such differences are usually significant. However, lack of similar data from the original description of *D. angulostoma* does not allow a comparison to be made. In the absence of this information and the otherwise similarity of the two groups of specimens, they are both designated as *D. angulostoma.*

Difflugia decloitrei Godeanu, 1972

Difflugia levanderi Playfair, 1918 (in part)
Difflugia acuminata Levander, 1894 (in part)

Description. The shell is transparent, ovoid, tapering evenly from the mid-body position towards the aperture and aboral extremity, there is the suggestion of a collar near the aperture due to the tapering ending prior to the apertural opening (Fig. 32a). In some specimens there is an apparent lateral compression, but it is usually slight and probably related to the fragility of the structure. It has a well defined outline, and the arrangement of flattish pieces of quartz give it a smooth surface. A network of organic cement is seen at most junctions of these particles (Fig. 32c). The mesh is about 280–350 nm in diameter and the walls 350 nm thick (Fig. 32d). The aperture is circular with often a rugged outline due to the placement of the flattish particles (Fig. 32b).

Measurements (in µm). Based on ten specimens: body length 77–95, breadth 39–55, diameter of aperture 20–27.

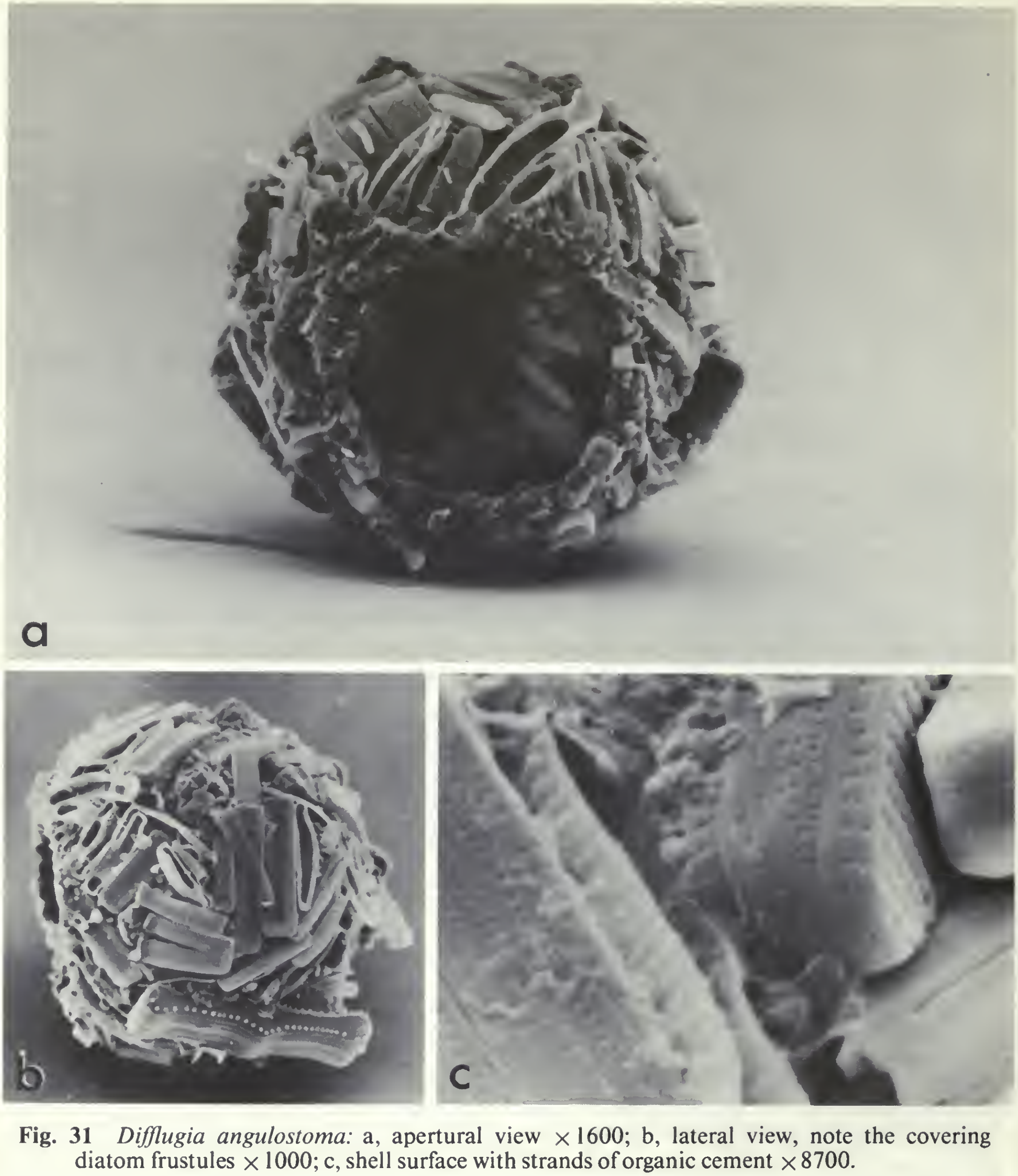

Fig. 31 *Difflugia angulostoma:* a, apertural view ×1600; b, lateral view, note the covering diatom frustules ×1000; c, shell surface with strands of organic cement ×8700.

MATERIAL EXAMINED. Specimens were collected from a sample of *Sphagnum* moss gathered at Myndd Hiraethog, Denbigh, Clywdd, North Wales in August, 1980.

GEOGRAPHICAL DISTRIBUTION. Australia (Playfair, 1918), Germany (Levander, 1894), Roumania (Godeanu, 1972).

REMARKS. Levander (1894) described four different forms of *D. acuminata,* one of which–type 'b'–was considered by Playfair (1918) to represent a distinct species., *D. levanderi.* Both of these authors suggested that there were two sizes of these specimens, '110×60 and 70×40 µm', the larger being rough and 'stony' whilst the smaller were chitinous with small, scattered granules. Recent descriptions of *D. levanderi,* for example

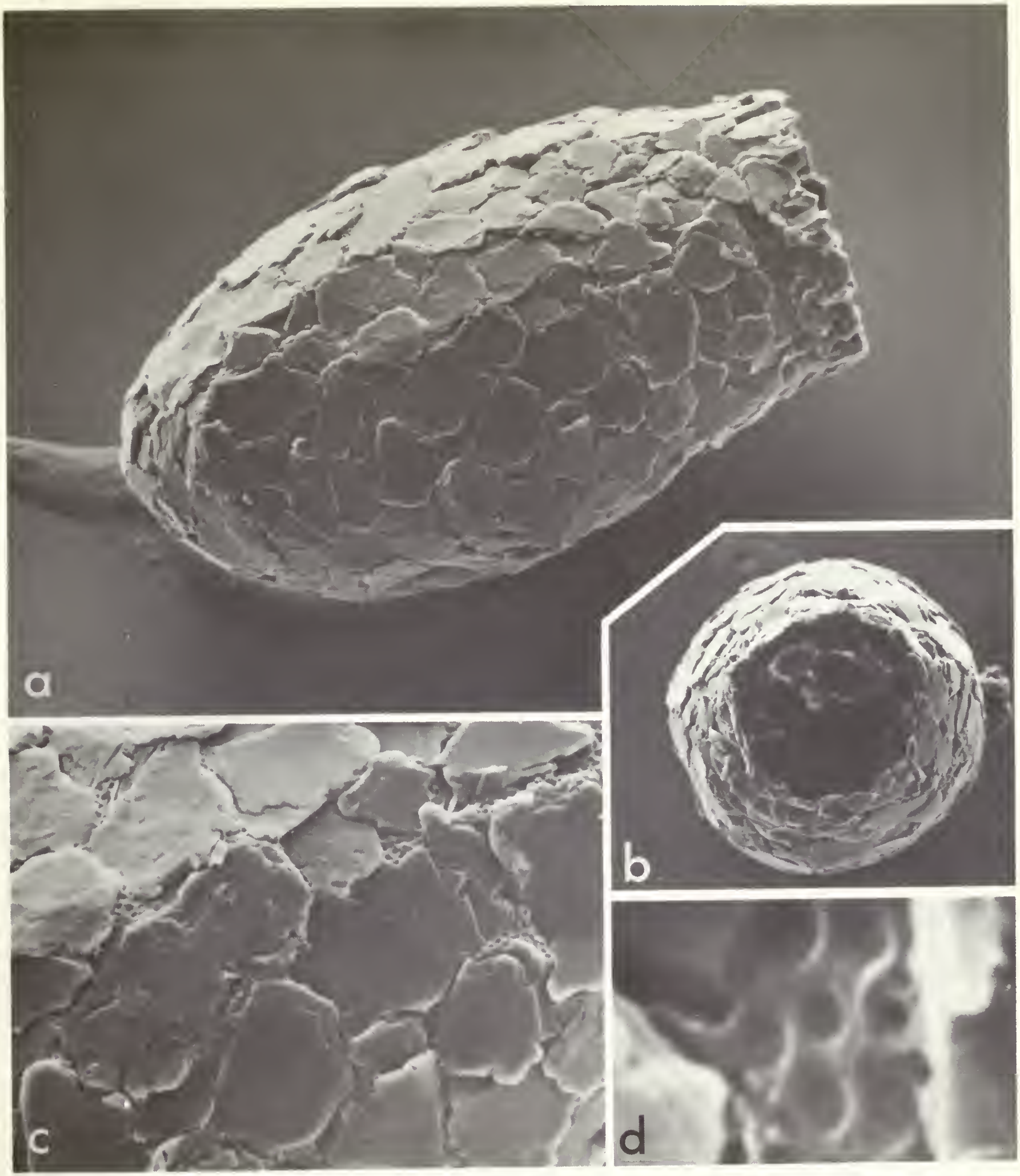

Fig. 32 *Difflugia decloitrei:* a, lateral view × 1300; b, apertural view × 900; c, portion of shell to show arrangement of flat particles to give a smooth surface × 2400; d, detail of organic cement network × 22 000.

that given by Gauthier-Lièvre & Thomas (1958) stated a range of body length of 85–140 µm suggesting that these are the larger specimens of the earlier authors. The specimens described by Godeanu (1972) as *D. decloitrei* appear to be similar to the group of smaller specimens, having a similar structure and large aperture. Those described here are in good agreement with this latter description and share similar measurements; body length 62–86, breadth 40–56 and diameter of aperture 20–23 (Godeanu, 1972). In the absence of larger shells for comparison the present specimens are referred to *D. decloitrei*.

Difflugia gramen Penard, 1902

This species has recently been redescribed (Ogden, 1980), but is included here because the numbers examined allow a comparison of dimensions between specimens from different habitats and localities. Both samples were collected in August, 1979, from sites which are about fifty miles apart. Specimens 'A' were selected from a sample of algae and water plants in stationary water (see Ogden, 1980), specimens 'B' from aquatic plants at the banks of the River Brett, near Hadleigh Suffolk, which in summer is a slow moving, small watercourse.

MEASUREMENTS (in μm). 'A' thirty-five specimens; 'B' forty-four specimens.

	body length	breadth	diameter of aperture	B/L	d/L	d/B
'A'	89–117	70–112	23–39	0·96±0·07	0·34±0·04	0·36±0·03
'B'	61–97	42–75	18–33	0·77±0·07	0·32±0·04	0·43±0·04
avg. 'A'	98·8	94·3	33·6			
avg. 'B'	78·7	60·5	26·2			

REMARKS. In shell construction the 'A' specimens are larger, spherical and more regular, only one aperture not appearing typically trilobed. Whilst, 'B' specimens are ovoid and nine (about 20%) had four lobes or were irregular in outline. It is interesting to note that the common feature between these specimens is the ratio of the aperture to the body length.

Difflugia masaruzzi Oye, 1958

DESCRIPTION. The shell is transparent, ovoid and composed of a mixture of flattish siliceous particles including some diatom frustules, to give a fragile structure with an irregular surface and outline (Fig. 33a). Organic cement is seen at some junctions (Fig. 33c), but there is a degree of overlapping with most particles. It appears as a network having a mesh of about 450–600 nm in diameter with walls 200 nm thick, each enclosure having a smaller network with a mesh about 90 nm in diameter (Fig. 33d). The aperture is circular, wide, usually with an irregular margin (Fig. 33b).

MEASUREMENTS. (in μm). Two specimens: body length 66–67, breadth 39–43, diameter of aperture 25.

MATERIAL EXAMINED. Specimens were collected from a sample of aquatic plants taken from the edge of a pond at Burley, New Forest, Hampshire in March, 1980.

GEOGRAPHICAL DISTRIBUTION. Congo (Oye, 1958), Costa Rica (Laminger, 1973a), Mexico (Laminger, 1973a).

REMARKS. In the initial description of *D. mazaruzii* it was stated by Oye (1958) to be similar to *D. rubescens* and *D. lucida*, although it only shares a transparent shell with these two species. The present specimens agree well with his description of a shell having some large distinct particles attached, and an aperture devoid of a regular margin more or less wavy because parts of the shell extend to the edge. Two specimens formed the basis for the earlier report and were somewhat larger, 72 and 78 μm in body length, 44 and 55 μm in breadth, 28 and 30 μm diameter of aperture. Although this species is similar in size to *D. glans* Penard, 1902 (see p. 7), it is distinct in having a transparent, fragile shell, wide aperture and a patterned organic cement.

Difflugia mica Frenzel, 1892

DESCRIPTION. The shell is brown, spherical or ovoid with a shallow apertural collar (Fig.

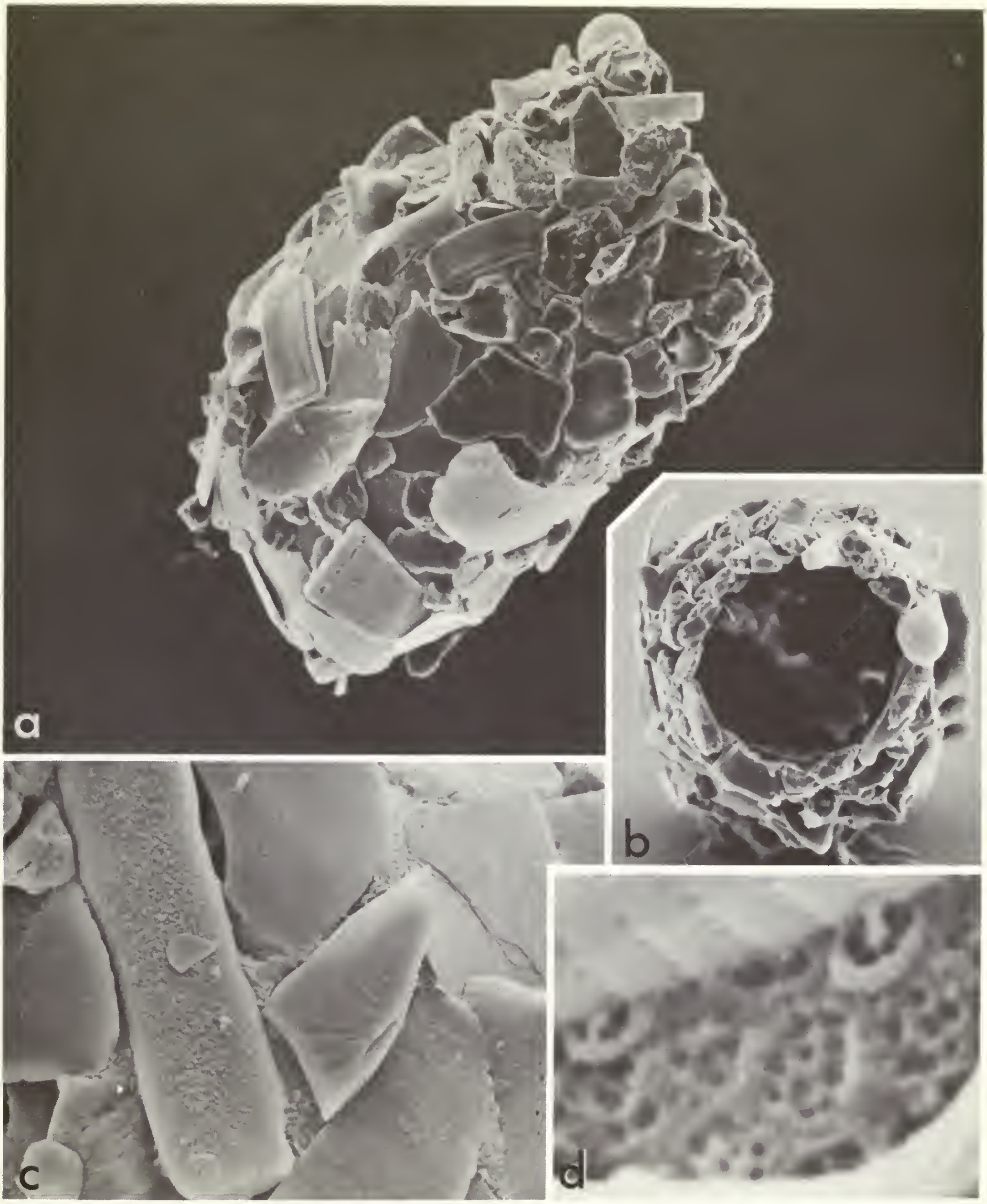

Fig. 33 *Difflugia masaruzii:* a, lateral view ×1400; b, apertural view ×1100; c, shell surface illustrating the distribution of organic cement ×4200; d, detail of organic cement network ×26 000.

34a). It is composed of small flattish pieces of quartz (Fig. 34d), packed tightly together to form a strong structure with a smooth surface and positive outline. Only small strands of organic cement are visible between the particles (Fig. 34e). The aperture is circular and usually well defined by the collar, which has a thin, even layer of organic cement around it

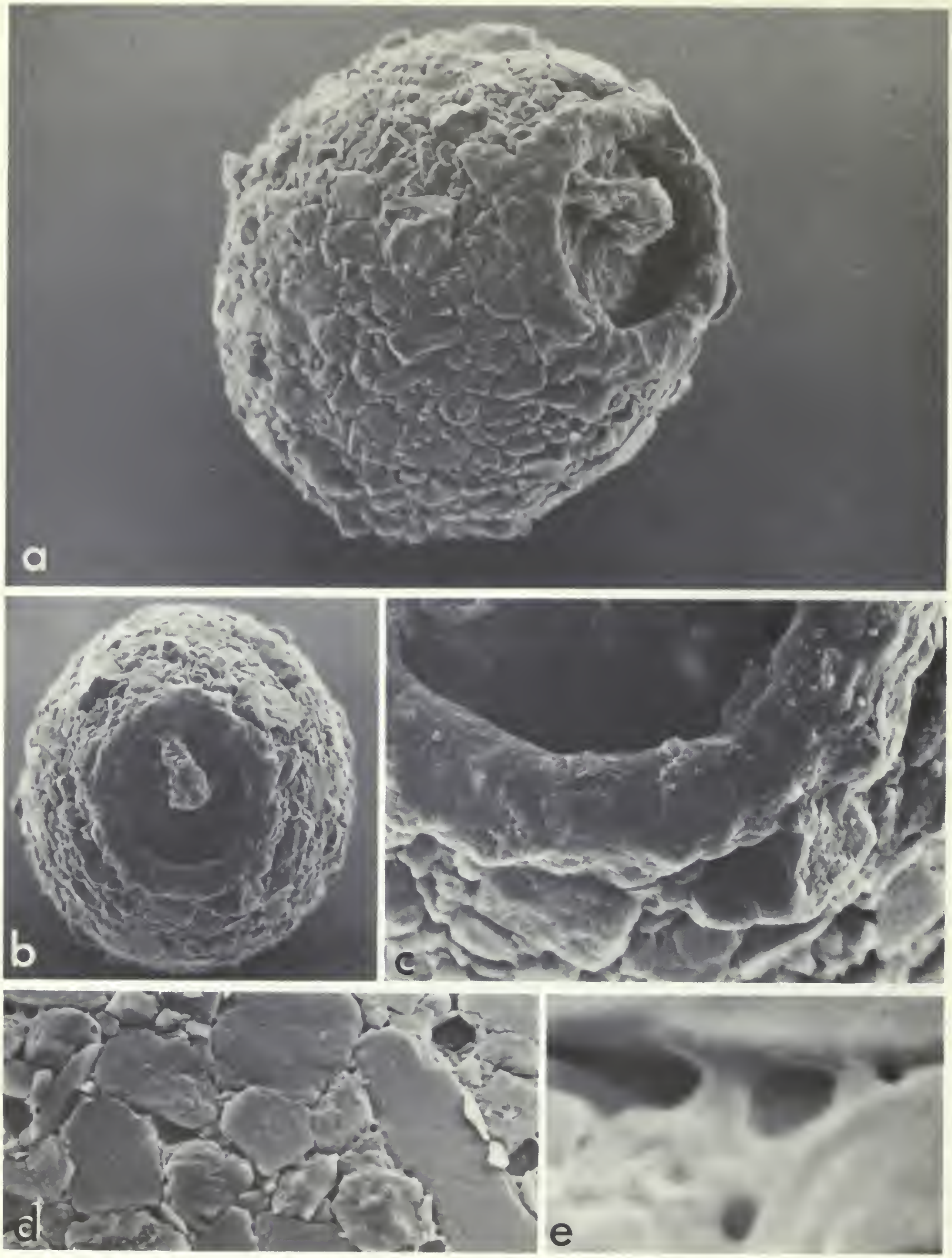

Fig. 34 *Difflugia mica:* a, latero-apertural view showing the shallow collar ×1600; b, apertural view, note that the aperture is blocked by a cyst plug ×1100; c, portion of apertural collar to illustrate the organic cement covering ×3900; d, shell surface with close packing of particles ×3800; e, detail of organic cement ×24 000.

(Figs. 34b & c). The illustrated specimen has a broken cyst membrane, made mainly of organic cement, just inside the apertural opening.

Measurements. (in µm). Based on seven specimens: body length 44–58, breadth 36–49, diameter of aperture 12–18; B/L 0·81 ±0·10, d/L 0·31 ±0·05.

Material examined. Specimens were collected from a sample of aquatic plants taken at the banks of the River Brett, near Hadleigh, Suffolk, in August, 1979.

Geographical distribution. Argentina (Frenzel, 1892), Germany (Schönborn, 1962*a* & *b*, 1965), Poland (Moraczewski, 1961, 1965); Roumania (Godeanu *et al.*, 1973), Switzerland (Penard, 1902).

Remarks. This species was initially described as *Difflugia* sp. by Frenzel (1892), the specific name being added as a footnote (p.135). In redescribing the species Penard (1902) used the name *D. mica?* Frenzel, the query has been dropped by subsequent authors and the name considered to be valid.

Difflugia microstoma (Thomas, 1954) comb. nov.

Difflugia globularis var. *microstoma* Thomas, 1954

Description. The shell is ovoid or subspherical, composed mainly of a mixture of small to medium pieces of flattish quartz and diatom frustules. The particles are arranged to give a relatively smooth outline (Fig. 35a), with the diatom frustules being in general additions to the main structure (Fig. 35d). The close packing of materials is such that only small strands of organic cement are seen (Fig. 35c). The aperture is circular and usually surrounded by a border of small particles (Figs. 35b & e).

Measurements (in µm). Based on fifteen specimens: body length 76–105, breadth 63–83, diameter of aperture 18–29; B/L 0·79 ±0·07, d/L 0·26 ±0·03.

Material examined. Specimens were collected from *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in July, 1978; March, 1980 and at Myndd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

Geographical distribution. Algeria (Gauthier-Lièvre & Thomas, 1958), France (Thomas, 1954).

Remarks. Thomas (1954) considered when describing the variety *D. globularis* var. *microstoma* that it was similar to specimens of *D. globulosa* illustrated by Penard (1902, p. 258 Fig. 6), although he later (Gauthier-Lièvre & Thomas, 1958) proposed both as synonyms of *D. minuta* Rampi, 1950. The examples of *D. minuta* described in this report show that *D. microstoma* is distinct in having a larger ovoid shell with a small aperture (compare ratios B/L and d/L, below), the latter feature also differentiates it from *D. globulosa* Dujardin, 1837.

Difflugia minuta Rampi, 1950

Description. The shell is ovoid or spherical, composed mainly of small pieces of flattish quartz and the occasional fragment or diatom frustule (Fig. 36a). The particles are packed so closely, to give a robust structure, that organic cement is visible only as small strands (Fig. 36c). The aperture is small and often surrounded by a narrow lip of organic cement (Fig. 36d), the lip is not apparent in side view but makes the apertural opening distinct when viewed *en face* (Figs. 36b & d).

Measurements. (in µm). Based on six specimens: body length 44–53, breadth 34–48, diameter of aperture 9–12; B/L 0·98 ±0·08, d/L 0·25 ±0·04.

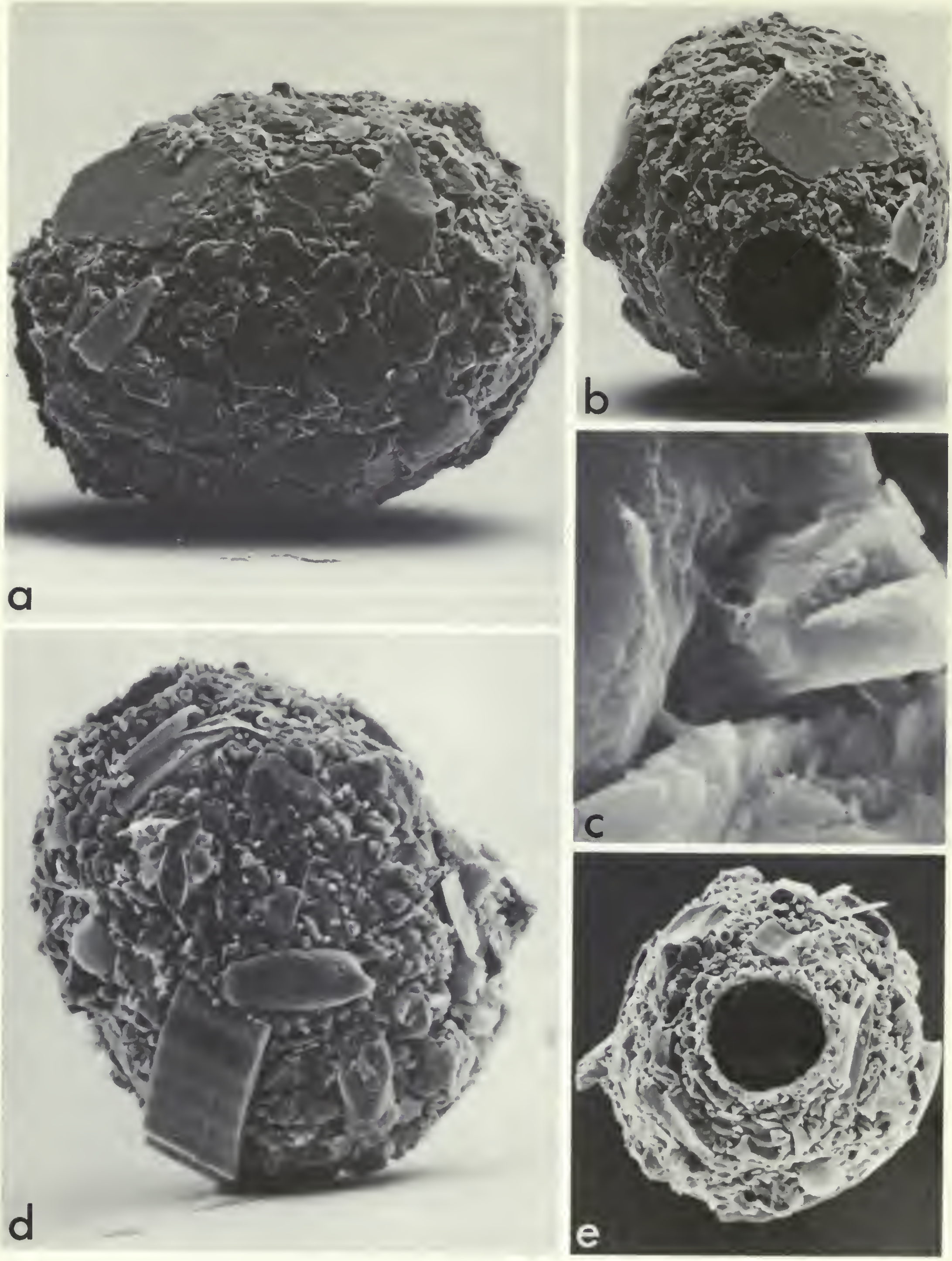

Fig. 35 *Difflugia microstoma:* a, lateral view of shell with smooth surface ×980; b, apertural view ×770; c, portion of shell surface with strands of organic cement ×13 000; d, lateral view of shell with added diatom frustules ×770; e, apertural view ×580.

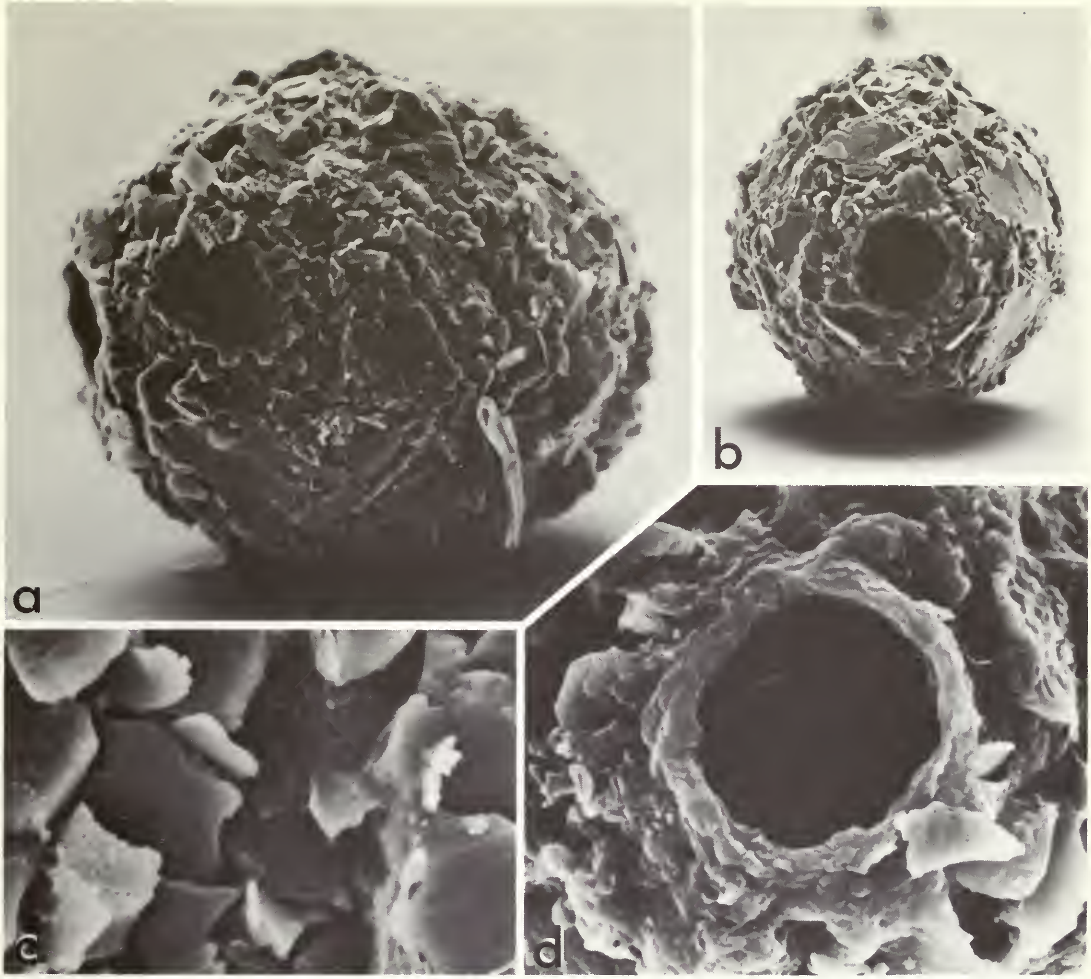

Fig. 36 *Difflugia minuta:* a, lateral view ×1400; b, apertural view ×970; c, portion of shell surface showing close packing of particles ×7700; d, detail of aperture to show narrow lip of organic cement ×3700.

MATERIAL EXAMINED. Specimens were collected from samples of *Sphagnum* moss gathered at three locations, Cranes Moor, in May, 1977; Holmsley, in July, 1978, both in the New Forest, Hampshire; Myndd Hiraethog, North Wales in August, 1980; and aquatic plants taken at the bank of a pond near Burley, New Forest in March, 1980.

GEOGRAPHICAL DISTRIBUTION. Brazil (Green, 1975), Costa Rica (Laminger, 1973*a*), Germany (Schönborn, 1965), Italy (Rampi, 1950), Roumania (Godeanu *et al.*, 1973).

REMARKS. The initial report (Rampi, 1950) of this species is brief, consisting of one figure and a few lines of description. These note that it has a globular shell made mainly of quartz particles and concludes that it differs from *D. globulosa* by its small size, length 53 µm, breadth 48 µm. Unfortunately no dimensions for the aperture are given. The specimens referred to this species by Gauthier-Lièvre & Thomas (1958) are all much larger than the measurements given by Rampi (1950), and are here considered to represent *D. microstoma* (see p. 53).

D. minuta is considered a distinct species in having a circular shell composed mainly of quartz, with a small aperture surrounded by a narrow lip or rim of organic cement.

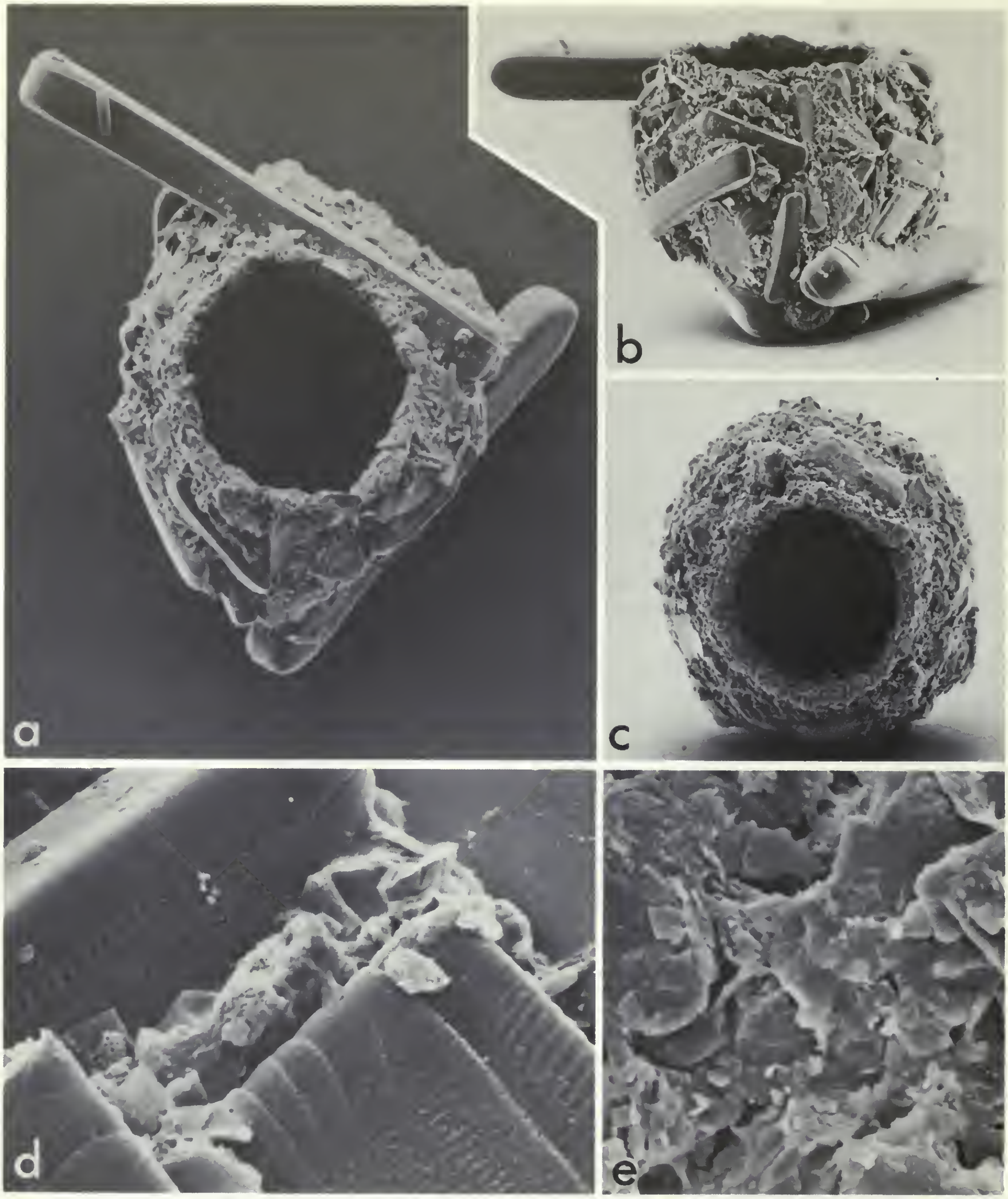

Fig. 37 *Difflugia rotunda:* a, apertural view ×270; b, lateral view ×240; c, apertural view of specimen made mainly of quartz particles, note the regular outline of the aperture ×290; d, portion of shell surface of 'diatom' specimen ×3300; e, shell surface of specimen made mainly of quartz ×2900.

Difflugia rotunda nom. nov.

Difflugia globularis var. *sphaerica* Chardez, 1956

Description. The shell is brownish, spherical or hemispherical, with the outline frequently distorted by the addition of large diatom frustules (Figs. 37a & b). The basic structure is made mainly of quartz (Fig. 37c), but diatom frustules or fragments of frustules, are often mixed with this in different proportions (Fig. 37b). This material is usually packed tightly together so that only small strands of cement are seen (Figs. 37d & e). The aperture is circular, sometimes slightly irregular, but usually surrounded by a shallow rim of small particles (Figs. 37a & c).

Measurements (in µm). Based on sixteen specimens: body length 133–204, breadth 138–193, diameter of aperture 79–113; B/L 0·98 ± 0·12, d/L 0·55 ± 0·07.

Material examined. Specimens were collected from samples of *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire in May, 1978; March, 1979; 1980 and Myndd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

Geographical distribution. Argentina (Vucetich, 1973*a* & *b*), Belgium (Chardez, 1956).

Remarks. In the original description of this variety, *D. globularis* var. *sphaerica*, Chardez (1956) noted that it differed in both size and diameter of aperture, the latter feature being about half the breadth, from his concept of *D. globularis*. According to Cash & Hopkinson (1909) the name *globularis* was used in error by Wallich (1864) for *D. globulosa* Dujardin, 1837. Nevertheless, these distinguishing features are used here to differentiate these specimens from other spherical species. Again a new name is proposed because the term *sphaerica* has been widely used for varieties in the terminology of this genus.

Etymology. The specific name has been chosen to reflect the shape of the shell (L. *rotunda* = round circular or orbicular).

Difflugia stoutii sp. nov.

Description. The shell is ovoid or ovoid elongate, composed of mainly small, flattish particles of siliceous material, including quartz, diatom frustules and shell plates from smaller testate amoebae (Figs. 38a & d). It is extremely fragile, several specimens having collapsed in preparation, and hence the apparent lateral flattening of the specimen shown in Fig. 38c. Organic cement is seen only as small threads due to the regular overlapping of the shell components (Fig. 38e). The aperture is roughly circular, small and appears to be recessed, but this latter feature may be due to structural fragility (Figs. 38b & d).

Measurements (in µm). Based on four specimens: body length 47–59, breadth 33–36, diameter of aperture 9–12.

Material examined. Specimens were collected from a sample of *Sphagnum* moss gathered at Myndd Hiraethog, Denbigh, Clwyd, North Wales in August, 1979.

Remarks. The present specimens are similar to three species recently described from Germany, namely *D. stechtinensis* Schönborn, 1962, *D. sudiformis* Schönborn, 1966 and *D. szczepanskii* Schönborn, 1965. They differ from the two former species in general dimensions, *D. stechtinensis* is almost spherical, with an aperturual diameter equal to half the body breadth, whilst *D. sudiformis* is an elongate, very slender species. *D. szczepanskii* is a slightly larger species but differs mainly in having an aperture size two-thirds of the body width. All three species are described as having a hyaline shell covered with a meagre scattering of particles.

D. stoutii is distinct in having a fragile, elongate ovoid shell composed of flattish particles and a small aperture.

Etymology. This species is named after the late Dr John Stout in recognition of his contributions to recent advances in protozoology.

Difflugia urceolata Carter, 1864

Description. The shell is opaque, ovoid or rotund, often having one or more irregular blunt

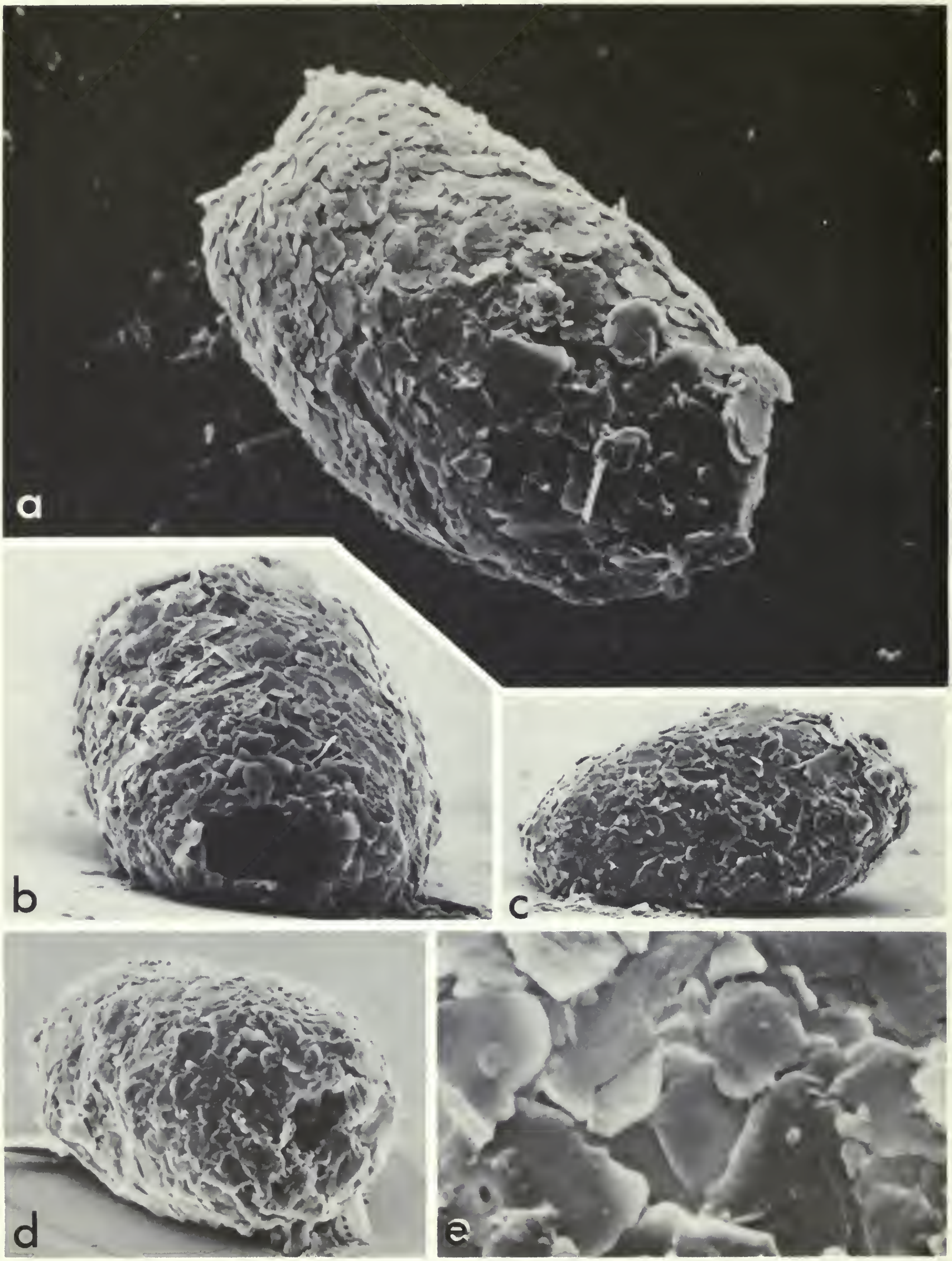

Fig. 38 *Difflugia stoutii:* a, lateral view ×1700; b, apertural view ×1700; c, lateral view of specimen slightly compressed anteriorly ×1100; d, latero-apertural view of ovoid specimen with slightly recessed aperture ×1300; e, shell surface, note the overlapping of particles ×5800.

aboral protruberances, and a pronounced apical rim or collar (Fig. 39a). The rim has a recurved appearance the edge of which is usually well defined (Figs. 39b & c), with an abundance of organic cement apparent as part of the rim matrix (Fig. 39e). The body is composed of small to medium particles of quartz, blended together so that the smaller particles and organic cement fill the gaps between the larger particles and give a relatively smooth surface. Diatom frustules or parts of them are occasionally included in the structure. Organic cement in the form of a network is seen as part of the matrix (Fig. 39d), the mesh has a diameter of about 240–290 nm with walls 100–180 nm thick (Fig. 39f). The aperture is usually circular (Fig. 39a).

Variation in this species is not uncommon. Although usually limited to the presence or absence of aboral protruberances, an occasional deformed shell may be seen. The specimen illustrated here (Figs. 40a & b) has a depressed apical rim, malformed body and defined aboral protruberances are absent.

MEASUREMENTS (in µm). Based on twenty-one specimens: body length 204–398, breadth 193–426, diameter of aperture 87–198; B/L 0·92 ± 0·10, d/L 0·44 ± 0·06.

MATERIAL EXAMINED. Specimens were collected from samples of *Sphagnum* moss gathered at Holmsley Lodge, Burley, New Forest, Hampshire on several occasions, May, 1977; 1978 and March, 1980.

GEOGRAPHICAL DISTRIBUTION. Algeria (Gauthier-Lièvre & Thomas, 1958), Argentina (Boltovskoy & Lena, 1971, 1974; Dioni, 1970; Vucetich, 1973*a* & *b*), Australia (Playfair, 1918), Austria (Laminger, 1972*c*, 1973*b*), Belgium (Chardez, 1960, 1961*b*; Chardez & Gaspar, 1976), Brazil (Green, 1975), British Isles (Cash & Hopkinson, 1909; Ogden & Hedley, 1980), Chile (Decloitre, 1954), China (Decloitre, 1954), Congo (Chardez, 1964; Štěpánek, 1963), Czechoslovakia (Štěpánek, 1952), France (Deflandre 1962b; Thomas, 1954), Germany (Jung, 1936), Hungary (Bereczky, 1973), Italy (Grandori & Grandori, 1934), Java (Bartoš, 1963*a*), Netherlands (Hoogenraad & Groot, 1940), Poland (Moraczewski, 1965), Russia (Kourov, 1925), Spain (Margalef, 1955), Sudan (Gauthier-Lièvre & Thomas, 1958), Switzerland (Penard, 1902), United States of America (Laminger *et al.,* 1979), Venezuela (Deflandre, 1926*a*; Grospietsch, 1975).

REMARKS. This is one of the most widely reported specimens of *Difflugia,* probably due to its size and distinctive shape. However, variation in shell construction has led to the description of several varieties. Thomas (1954) used the presence of aboral protruberances to differentiate the variety *olla* Leidy, 1879; whilst Gauthier-Lièvre & Thomas (1958) list four which differed in rim construction, namely *lageniformis* (Wallich), *lageniformis* forma *minor* forma nov., *minor* Deflandre and *sphaerica* Playfair; and more recently descriptions of specimens which differed in shape and material have produced two more-var. *chayuensis* Wang Jiagi, 1977 and forma *subureceola* Chardez & Gaspar, 1976.

These reports of natural variation can have little value until they are thoroughly investigated, and the present specimens are therefore referred to *D. urceolata.*

Compressed species

Difflugia hiraethogii sp. nov.

DESCRIPTION. The shell is light yellow or transparent, thin pyriform with a distinct neck or collar which often has parallel sides (Figs. 41a & b). The neck region is made of angular quartz and usually has a rough appearance (Fig. 41b), whilst the remainder of the body is composed of small to medium pieces of flattened quartz and has a smooth appearance. Organic cement is frequently seen in small areas as part of the shell matrix (Fig. 41d). It is in the form of a network, made of fused rings each having an internal diameter of about 250–320 nm and walls 200–260 nm thick (Fig. 41e). The aperture is circular and surrounded by assorted particles of quartz to give it an irregular outline (Fig. 41c).

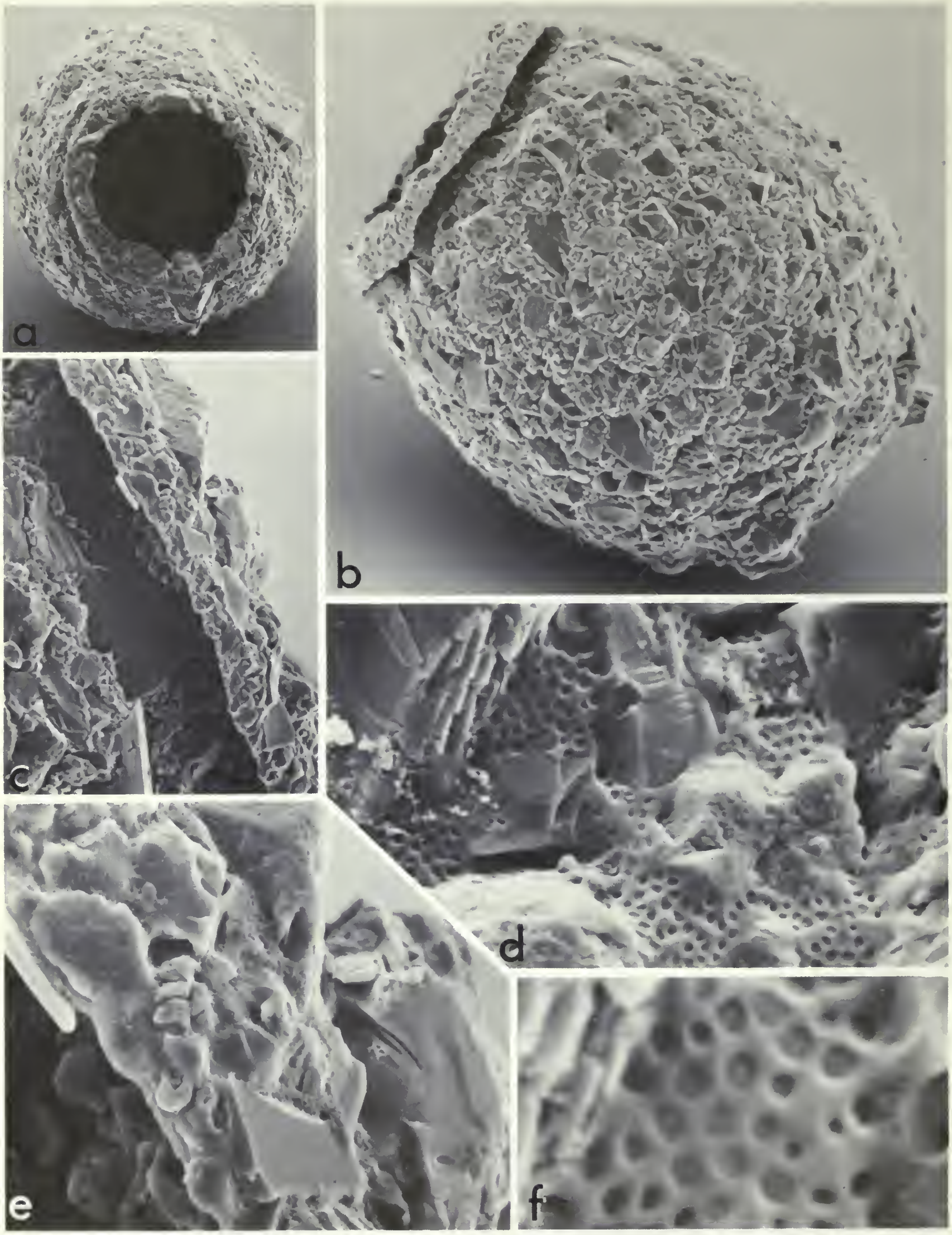

Fig. 39 *Difflugia urceolata:* a, apertural view × 180; b, lateral view, note the apertural collar and small aboral protruberances ×260; c, part of apertural collar, note the well-defined edge of small particles ×790; d, portion of shell surface to illustrate the distribution of organic cement ×5600; e, detail of apertural collar shown in c. ×3700; f, detail or organic cement network ×15 000.

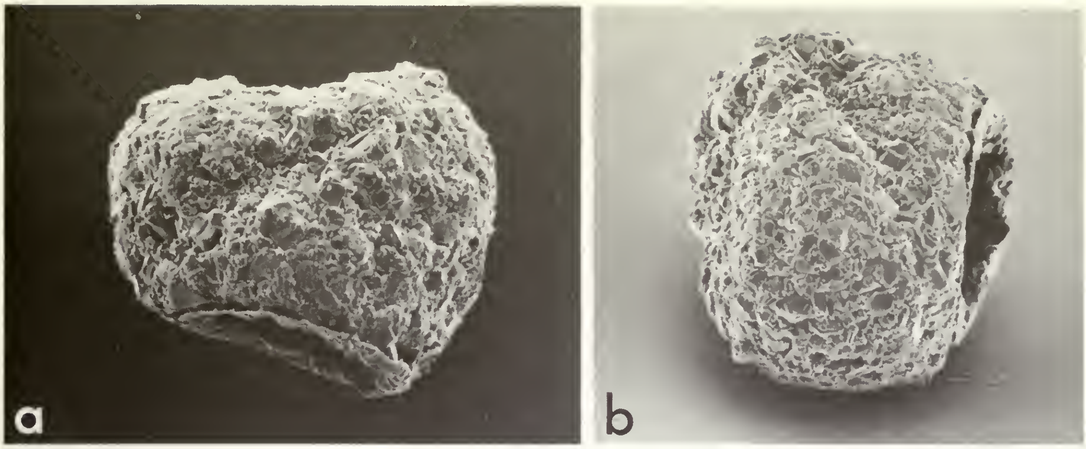

Fig. 40 *Difflugia urceolata* specimen with a deformed shell; a, lateral view ×170; b, latero-apertural view ×160.

Some of the examined specimens had cyst plugs in their apertural openings. These plugs varied from being either an uneven mixture of angular quartz (Fig. 42a) or flattish pieces (Fig. 42b), in both instances the sealing cement was similar to that binding the shell walls (Figs. 42c & d).

MEASUREMENTS (in µm). Based on twenty-six specimens: body length 137–171, breadth 87–137, depth 57–84 diameter of aperture 35–52; B/L 0·67 ±0·06, d/L 0·26 ±0·02.

MATERIAL EXAMINED. Specimens were collected from a sample of *Sphagnum* moss gathered at Myndd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

REMARKS. This species is similar to two other compressed species namely, *D. compressa*? and *D. lingula* Penard, 1911. Complications regarding the species *D. compressa* Carter, 1864 should have been resolved by Cash & Hopkinson (1909) who suggested that from Carter's figures he was 'beyond question' referring to a species of *Pontigulasia*. Nevertheless, the name has been used subsequently to refer to compressed specimens of *Difflugia*, either as *D. compressa* or *D. oblonga/pyriformis* var *compressa*. Whether or not there are some genuine specimens of *Difflugia* amongst these descriptions is difficult to know, but the name *compressa* is preoccupied by Carter's description and is no longer valid, and most refer to much longer, broader specimens than those described here. The present specimens are distinct from *D. lingula* Penard, 1911 and *D. lingula* var *regularis* Gauthier-Lièvre & Thomas, 1958 because these have a more rounded shape which tapers sharply from the mid-body region to the aperture, and *D. lingula* also has an aboral horn.

D. hiraethogii can be recognised by its lateral compression, distinct circular collar and aperture.

ETYMOLOGY. This species is named after the area of North Wales in which it was found.

Difflugia lucida Penard, 1890

DESCRIPTION. The shell is transparent, ovoid, gracefully curved aborally but tapering more gradually towards the aperture to give a well defined outline (Fig. 43a), and laterally compressed (Fig. 43c). It is thin, smooth and composed mainly of flattish pieces of quartz with an occasional siliceous shell plate or diatom frustule added, these particles are usually arranged so that they meet but do not overlap. Small areas of organic cement, in the form of a network, are seen as part of the shell matrix (Fig. 43d). The network is often an arrangement

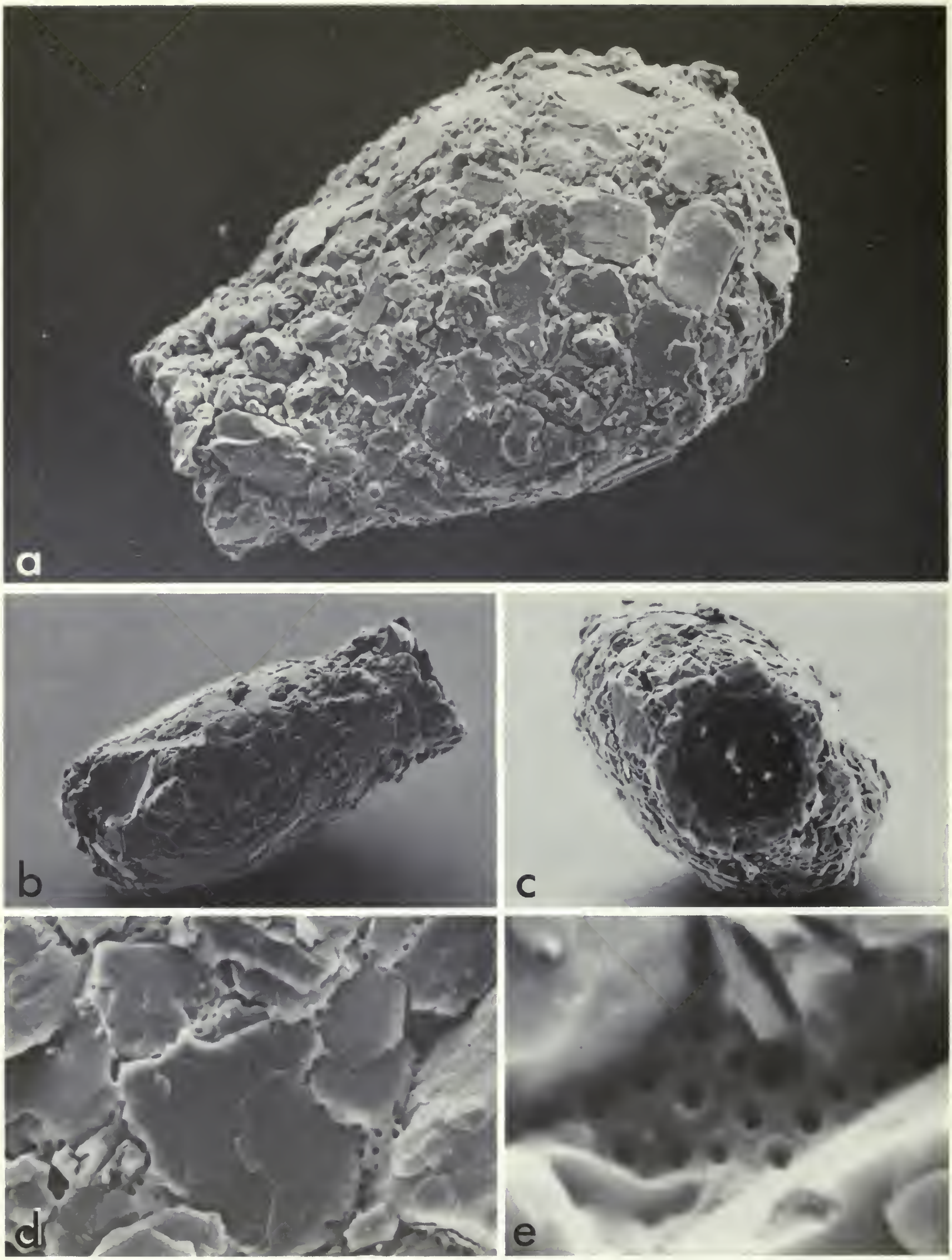

Fig. 41 *Difflugia hiraethogii:* a, lateral view ×730; b, lateral view to illustrate the distinct circular neck and compressed body ×430; c, apertural view ×540; d, portion of shell surface showing small areas of organic cement ×3500; e, detail of organic cement ×13 000.

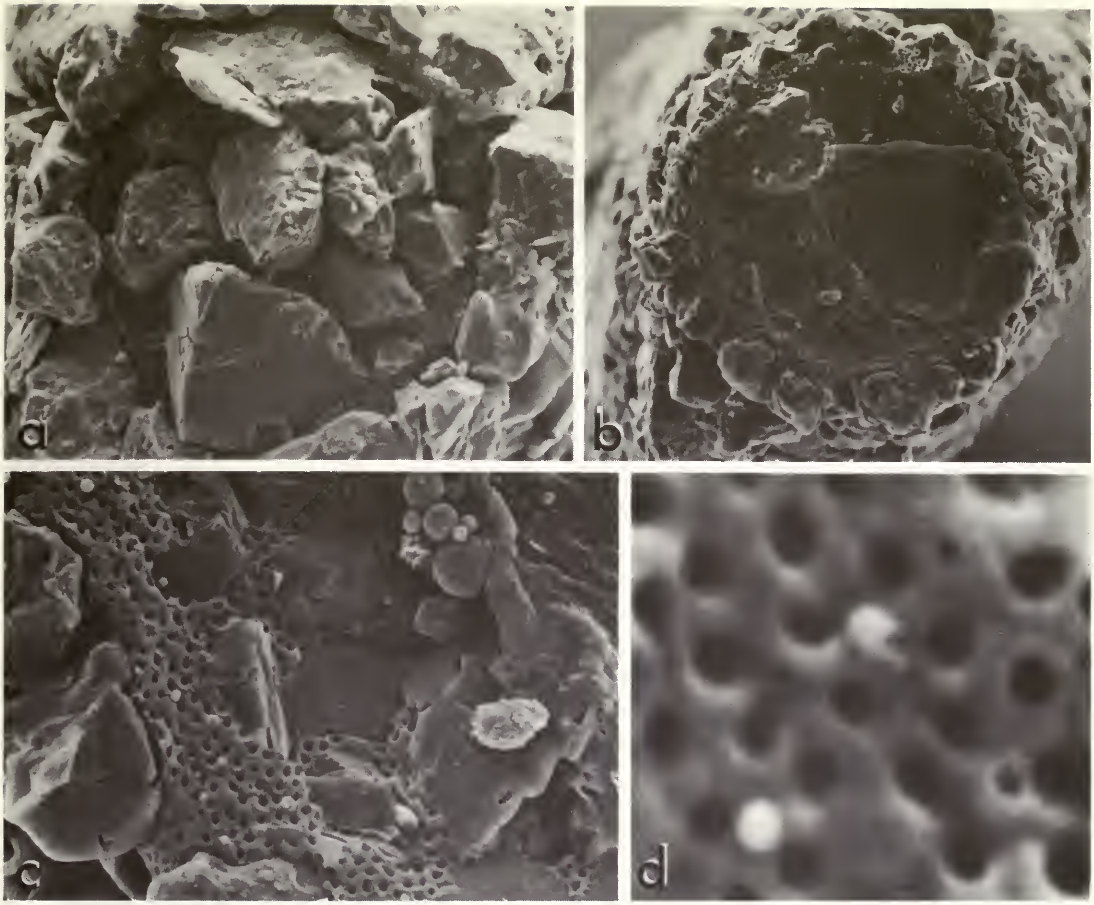

Fig. 42 *Difflugia hiraethogii:* a, detail of aperture with cyst plug composed mainly of angular quartz, organic cement at edges × 1500; b, specimen with cyst plug composed mainly of organic cement × 1100; c, portion of cyst plug shown in b., note that the particles appear to be well embedded in organic cement × 3500; d, detail of organic cement of cyst plug × 17 000.

of rings whose internal diameter is about 380–480 nm with walls 95–125 nm thick (Fig. 43e). The aperture is elliptical and surrounded by irregularly arranged particles which give a rough outline to the immediate apertural region (Figs. 43a & b).

Several presumably encysted specimens were present in the sample, and easily distinguished optically by the dark appearance around the aperture. On detailed examination this dark area was seen to be a concentration of flat particles projecting from the apertural openings (Figs. 44a & b).

Measurements (in µm). Based on thirty-six specimens: body length 67–91, breadth 40–55, depth 23–37, diameter of aperture 23–29, depth of aperture 13–19.

Material examined. Specimens were collected from a sample of *Sphagnum* gathered at Myndd Hiraethog, Denbigh, Clwyd, North Wales in August, 1980.

Geographical distribution. Algeria (Gauthier-Lièvre & Thomas, 1958), Argentina (Vucetich, 1972), Austria (Laminger, 1972*a*, 1973*b*, 1974, 1975), Belgium (Chardez, 1961*b*; Couteaux, 1969), British Isles (Cash & Hopkinson, 1909), Bulgaria (Golemansky, 1967), Canary Isles (Gracia, 1965*a* & *b*), China (Bartoš 1963*b*), Congo (Chardez, 1964; Štěpánek, 1963), Costa Rica (Laminger, 1973*a*), Czechoslovakia (Rosa, 1957; Štěpánek, 1952, 1967),

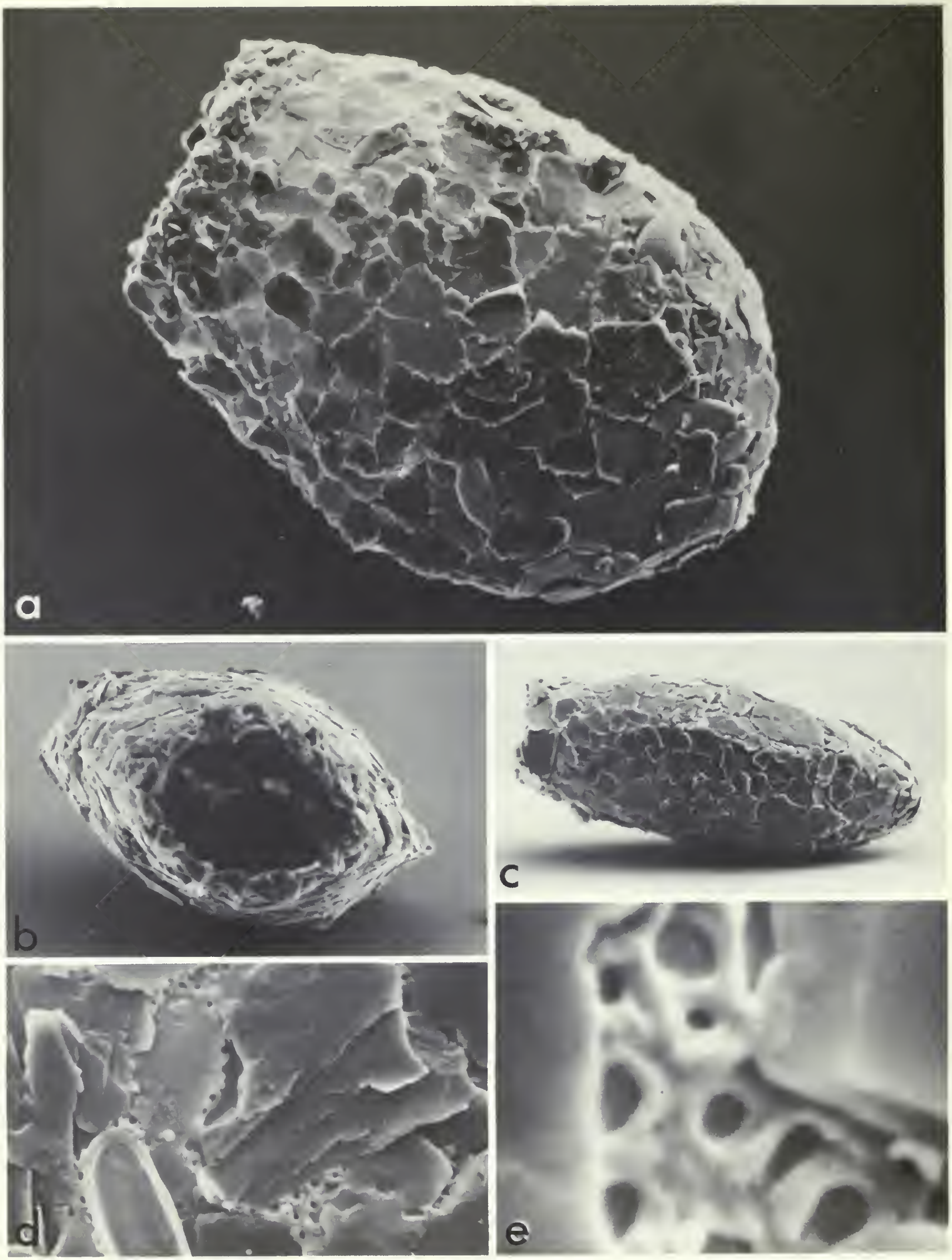

Fig. 43 *Difflugia lucida:* a, lateral view to illustrate basic outline ×1300; b, apertural view ×1100; c, view showing lateral compression and smooth surface ×840; d, part of shell surface with small areas of organic cement ×5900; e, detail of organic cement network ×23 000.

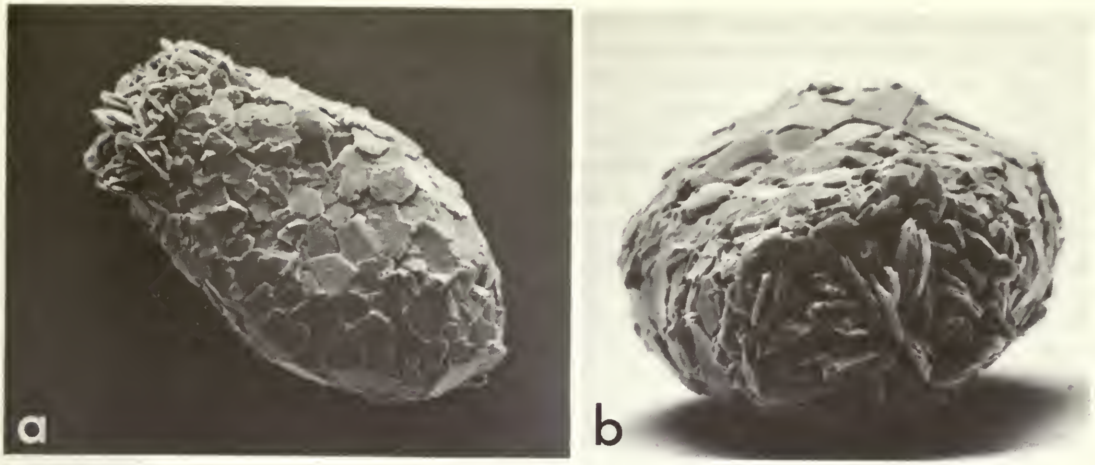

Fig. 44 *Difflugia lucida* specimen with cyst plug, note the irregular arrangement of particles in the apertural opening: a, lateral view ×620; b, apertural view ×1100.

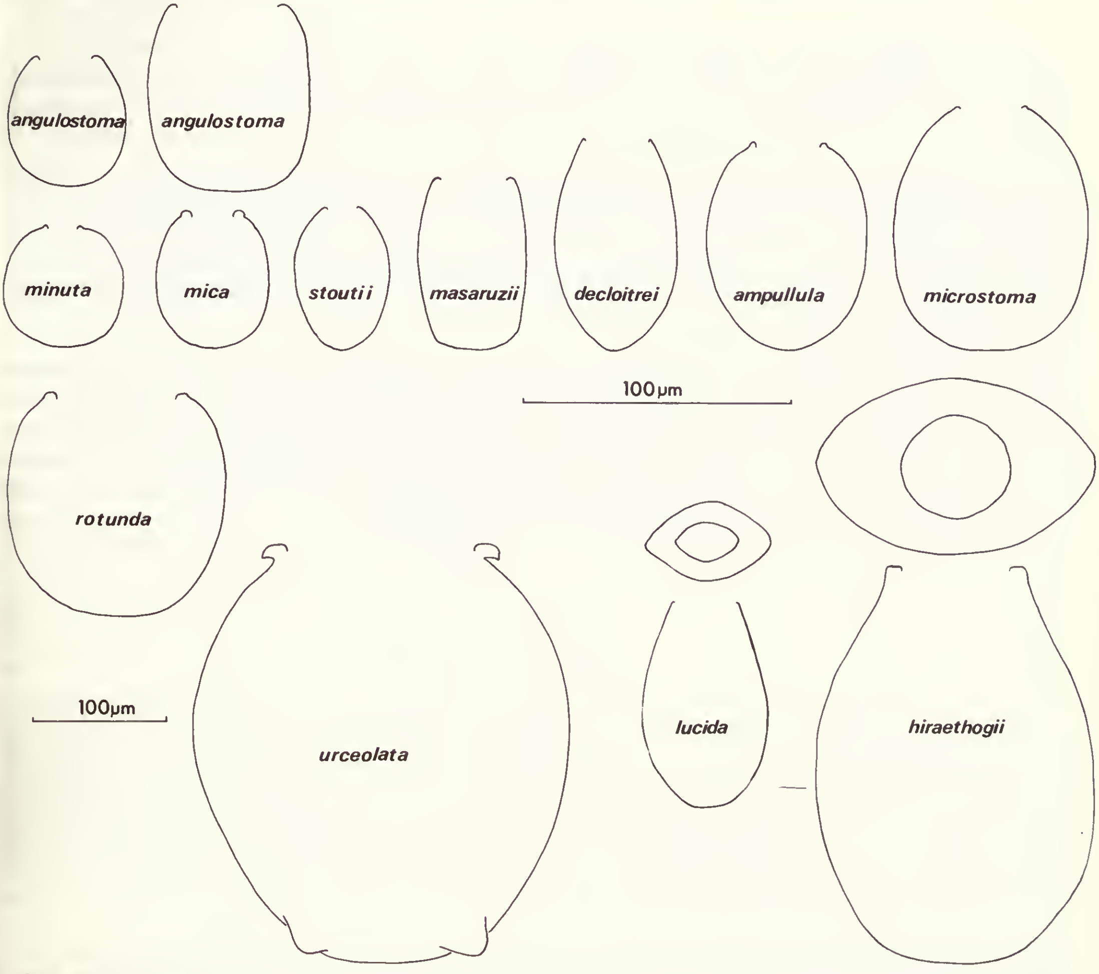
angulostoma
angulostoma
minuta
mica
stoutii
masaruzii
decloitrei
ampullula
microstoma
100µm
rotunda
100µm
urceolata
lucida
hiraethogii

Fig. 45 Diagrams of ovoid, spherical and compressed species to illustrate the basic outline, based on measurements given in Table 4. Note that *D. rotunda* and *D. urceolata* are drawn to the reduced scale.

Table 4 Average dimensions of ovoid or spherical species and compressed species used to give basic outlines illustrated in Fig. 45

Species	Length	Breadth	Diameter of aperture	
angulostoma a.	48	45	20	
b.	68	58	38	
minuta	45	44	11	
mica	51	41	16	
stoutii	53	34	11	
masaruzii	66	41	25	
decloitrei	79	45	24	
ampululla	77	59	25	
microstoma	91	72	23	
rotunda	165	159	90	
urceolata	314	283	143	
	length	breadth	depth	diameter of aperture
lucida	76	46	30	17×25
hiraethogii	150	104	67	41

France (Thomas, 1954), Germany (Schönborn, 1962*a* & *b*), Guatemala (Laminger, 1973*a*), Hungary (Varga, 1963), Italy (Grandori & Grandori, 1943; Rampi, 1950), Java (Bartoš, 1963*a*; Hoogenraad & Groot, 1940*b*), Mexico (Laminger, 1973*a*), Morocco (Decloitre, 1961), Nepal (Laminger, 1972*b*), Netherlands (Hoogenraad & Groot, 1940*a*), Poland (Golemansky, 1970; Pateff, 1926), South Shetland Isles (Smith, 1972), Spain (Gracia, 1964), Switzerland (Penard, 1902).

REMARKS. Some differences in dimensions are worth noting from earlier descriptions; Penard (1890) gave a range of body length 50–70 µm, but later stated that specimens ranged between 50–60 and rarely greater than 65 µm (Penard, 1902), Cash & Hopkinson quoted 60–80 µm, whilst Gauthier-Lièvre & Thomas (1958) suggested that there might be three groups (a) 44–50 (b) 55–70 (c) 83–90. In the present group of specimens only seven are outside of the range 70–80 µm and they are remarkable for their similarity.

This species is distinct in having a well defined shape and by being evenly compressed.

Discussion

One of the main difficulties encountered in trying to identify specimens of *Difflugia* is due to the irregular shape of the shell. It is a problem shared with other agglutinate species of protozoa, such as the foraminifera. In general most species have a regular basic outline, which may be altered by either natural variation or obscured by the addition of extraneous material. Both natural and additional variation are probably related to the composition of the shell, fragile shells being more likely to be influenced by disturbances in the environment during or after construction, whilst robust shells may be so encrusted by particles that any resemblance of a specific shape is lost.

Fragile shells are usually made of small particles arranged in a single layer and often have organic cement as a major component of the shell matrix. In some species a smooth surface composed of flattish particles is constructed, for example *D. mamillaris,* where variation in general shape is frequently seen especially in the aboral region (see Fig. 23). Nevertheless, in a species with a similar surface but different shape, *D. lanceolata* which is rounded rather than pointed in the aboral region, there is a relatively constant shape. In the present report a third of the specimens of *D. mamillaris* differ from the basic outline given in Fig. 29, whilst all of the specimens of *D. lanceolata* agree with the outline in Fig. 18. Although robust shells are usually made of angular quartz which do not lend themselves to being arranged in a regular manner, if enough specimens of a species is present in a sample it is possible to illustrate a basic outline. The problems of subsequent recognition of such species from the basic outline is complicated when the diagnostic feature is obscured by the arrangement of particles. For instance the diagnostic feature may be the presence of a neck, but if this is hidden it may be identified incorrectly. Amongst species with this type of shell, examples of specimens incorporating a single large particle with similar dimensions to the whole shell have been observed and a not infrequent sight is to see two similar shells united. In these latter instances the shell is usually of similar size and composition, but these are not necessarily species of *Difflugia* but can be other agglutinate forms like *Pontigulasia* (pers. observation).

To assist in resolving the question of what represents the basic outline in the species described here, three sets of line drawings are provided (Figs. 18, 29, 45) which are based on the average dimensions of the specimens examined.

In the previous studies on pyriform species of *Difflugia* it has been suggested (Ogden, 1979) that measurements are useful in distinguishing species, with the body length and diameter of aperture perhaps being the more stable dimensions. However, it was emphasised that these features alone are not usually sufficient to warrant specific diagnoses. The problem of using dimensions as a diagnostic character is that they may be valid for a proportion of species in a genus, but do not hold for all especially in the present instance with a genus supposedly comprised of over three hundred species. Possibly this is best illustrated by the variability in size exhibited within a species of testate amoebae, the smallest often being reported as half the size of the largest, which does not pose problems of identification when the body length is under 80 μm, but for those of larger dimensions the difference between 200 μm and 400 μm can often be interpreted as representing two separate species. The extreme example is as we have noted previously (Ogden & Fairman, 1979) the range of measurements quoted for the body length of *D. oblonga,* 60–580 μm, which is so variable that it could embrace most of the genus or almost all of the described testate amoebae. Nevertheless, there are examples of consistent dimensions within a species, for instance those of *D. lanceolata* and *D. mamillaris* described here are in good agreement with previously published results (Penard, 1902; Grospietsch, 1957). The regularity of body length in *D. lanceolata* is such that over 87% of the specimens fall within a range of ± 10% of the average value given in Table 2, whilst in *D. mamillaris* 96% fall within the same range.

Ovoid or spherical specimens of *Difflugia* present the same problem. In certain cases groups of similar species may only be distinguished by dimensions, for example *D. anchlora, D. gramen* and *D. lobostoma* (see Ogden, 1980) which may represent a phylogenetic series. Whilst is other cases, like the *D. globulosa/globularis* species complex, size variation is so great that it is difficult not to include any ovoid or spherical specimen between 50–150 μm in this complex. Part of the difficulty is illustrated by the two groups of specimens described here as *D. angulostoma* (p. 47), where the shells are identical in construction and essentially they share the same shape, but there are differences in dimensions especially the diameter of the aperture. It is possible to separate some of these small spherical species using the latter feature in addition to other differences, as shown in the descriptions of *D. minuta, D. mica* and *D. microstoma* (see p. 53, p. 50 & p. 53). Structural differences in basic outline as mentioned earlier are mainly related to shell components and deformities, the former concerns the choice of materials and will be dealt with later, but the latter using *D. urceolata* as an example may be due to its large size. Perhaps it is easier to understand if one considers that in all probability the shell components are not cemented together until the final shape has been moulded by cytoplasmic movements. As this process takes about sixty minutes in a small siliceous species (Ogden, 1981), it will probably take considerably longer in a larger animal, during which time in a natural environment there is a continual motion and hence a possibility of disruption. The result of such a disturbance may produce the shell illustrated in Fig. 40, sufficiently different from normal but not enough for the animal to abhort and discard the shell prior to the final stiffening of the cement.

Studies on clonal cultures of both siliceous and proteinaceous species (Ogden, 1981 & pers. observations) show that variation in dimensions are small, differences outside the norm usually being attributed to abnormal development and even here it is usually below 5%. Such abnormal development is thought to be associated with cultural differences and not a frequent natural occurrence. One feature of siliceous species behaviour which may explain some changes in dimensions, is the occasional production of a shell having a double complement of shell plates (Hedley & Ogden, 1973). However, this results in an increase in volume of an ovoid structure, which means that the enlargement in body length is probably no greater than a third.

At present there are only two reports (Jennings, 1916, 1937) on the development of *Difflugila corona* in the laboratory. Both have shown that there can be some variation in shell construction and until further observations are available on other species of *Difflugia*, the question of shell size and composition as diagnostic features will remain a subject of speculation.

Mention has already been made in the literature of differences in shell construction and the three categories which are readily identified, robust, intermediate and fragile (Ogden, 1980). But the choice of materials, other than a comment (Ogden, 1980) on the influence of pH, has not been discussed. That a system of choice is available to the animal is clearly demonstrated by the composition of certain shells. For example, *D. minutissima, D. lanceolata, D. mamillaris* and *D. decloitrei* all use flattish pieces of quartz, in some instances small flat particles of diatom frustules may be substituted, but the components used appear to be restricted in size and thickness. The function of the cytoplasm to identify and select these particles may appear to be extreme. Nevertheless, it can be measured against the ability of siliceous testate amoebae to hold each shell plate during shell construction, place it in position so that there is an even amount of overlap between plates and in some specimens manipulate spines into definite positions (Ogden, 1981). This selectivity is not restricted to flat particles, but probably includes the choice of diatoms or angular particles, as well as mixtures of all types in the composition of *Difflugia* shells. An additional factor that influences the choice of particles is undoubtedly the structure and extent of organic cement in the shell matrix.

It has already been suggested (Ekert & McGee-Russell, 1974) that the organic cement which binds the shell particles together in *Difflugia lobostoma* imparts both strength and flexibility to the structure. This may seem obvious from the different type of shells constructed by these animals, but it has an importance related to the material used. For instance, when the cement becomes part of the surface matrix, usually in species with flat particles, it is found at each facet as part of the shell wall. The strength of the shell is then directly related to the tenacity of the cement at these junctions.

Furthermore, in species where there is some overlapping of particles the cement is interwoven with the material and can be likened to the structure of a brick wall, in which the strength is dramatically increased by the combination of bricks and mortar beyond the strength of the individual materials assessed on their own. The importance of the organic cement in shell structure is easily demonstrated by treating a robust individual with either a chelating agent or concentrated sulphuric acid, in each case within a short time it is reduced to a small residue of particles. Strength is not directly due to the composition of the acid mucopolysaccharide material that forms the basic organic cement, but to the properties of this material. It has already been shown that inorganic elements incorporated with this type of material in the proteinaceous shells of testate amoebae (Hedley *et al.,* 1976; pers. observ.)

and areanceous foraminifera (Hedley, 1963) are thought to strengthen the shell. Some specimens of *Difflugia* have been examined by X-ray microanalytical techniques (pers. observ.), and found to have a significant amount of ferrous iron associated with areas of organic cement. This probably accounts for the reports of yellow or brown specimens, the degree of colouration being proportional to the amount of inorganic elements bound to the organic cement. There is no doubt that the density of this colouration in proteinaceous specimens can be used as a measure of the degree of reinforcement that the inorganic elements impart to the structure, newly formed shells being light coloured and fragile, whilst older shells are dark and strong. This measure can probably be applied to agglutinate forms as well.

The differences in the network structure of the organic cement are harder to understand, especially as the examination is limited to surface detail. A need for porosity in some of the individual organic cement units is puzzling. If they are definite pores to the interior of the shell they might function as pressure valves for aqueous interchange, because often when the animal is moving or feeding the apertural opening is completely blocked by cytoplasmic extrusions. Such a scheme could ensure that the internal volume unoccupied by cytoplasm is not isolated and allowed to stagnate. Alternatively it may be associated with the hardening process by inorganic elements. This process seems to be directly related to the environment and the chemical composition of the cement, the activities of the animal apparently having no effect on this association. The strengthening process has some degree of justification because the pores often seen between individual proteinaceous units is newly-formed, light coloured, shells of *Arcella,* are not seen in older darker specimens. Examination of the walls of such specimens show that they are thick and stronger, the implication being that the inorganic elements have strengthened the shell not the deposition of further organic material (pers. observ.).

The diversity in the construction of the organic cement units is considered to be a good taxonomic feature, although they are beyond the limit of optical microscopy, the appearance of some being particularly unique for example the button-type of *D. lacustris* (see Fig. 5e p. 9). The sharing of the same type of unit between different species may suggest some phylogenetic relationship, possibly linked to the type of shell construction whether smooth, rough, fragile or strong. However, at present only a quarter of the described species have been examined and it is too early to make proposals on such relationships. That is apart from the apparent sharing of the same organic cement pattern between most ovoid species. It is hoped that further studies in progress on this genus will help to unravel the complications attributed to describing so many different shapes and forms, and allow a comprehensive division based on shell structure.

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British Museum (Natural History)

An Atlas of Freshwater Testate Amoebae

C. G. Ogden & R. H. Hedley

1980, Hardcovers, 222pp, £17.50 (£18.00 by post). Co-published by British Museum (Natural History) and Oxford University Press.

This book illustrates, using scanning electron micrographs, most of the common species of testate amoebae that are found in freshwater habitats. Information on the biology, ecology, geographical distribution and a classification are followed by descriptions of ninety-five species. Each of these is illustrated by several views of the shell.
The text is designed not only to enable biologists to identify species of testate amoebae, but to serve as an introduction to students interested in the taxonomy and biology of these freshwater protozoa. It will be of special interest to protozoologists, ecologists, limnologists, water treatment specialists and micropalaeontologists interested in recent sediments.

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Cirolana cranchi Leach, 1818 (Crustacea: Isopoda: Cirolanidae) redescribed, with notes on its distribution

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Cirolana cranchi is considered to be the type of the genus *Cirolana* Leach (by monotypy, Bruce, 1981) and as *Cirolana* is the type genus for the family Cirolanidae (Harger, 1880; Hansen, 1890), the species is of some significance. It comes therefore as some surprise to find that *C. cranchi* has not been effectively described since the work of Hansen (1890). The species has frequently been considered to be indistinguishable from *Cirolana parva* Hansen 1890 (Stebbing, 1917; Nordenstam, 1946; Monod, 1976), and though these authors have discussed at some length the similarities of the two species, none resorted to redescription.

Hale (1925) described a variety of *Cirolana cranchi* from South Australia. Examination of that species suggested that not only was Hale's variety quite distinct from *C. cranchi,* but that several closely similar species exist in the seas around Australia. It was therefore necessary to examine the holotype and specimens of *Cirolana cranchi* from England in order to be certain that none of the Australian species is *C. cranchi.*

To prevent any further confusion of *Cirolana cranchi* with *C. parva* and similar related species, a new description is given here with full figures, from specimens in the British Museum (Natural History) collections. The holotype, initially stored in the British Museum's dry collections (Ellis, 1981) is in extremely poor condition, lacking most appendages, setae and spines, and is in two pieces. The holotype, taken from Cornwall was closely compared to Norman's (1904) specimen to assure conspecificity, and the description and drawings are taken from the latter.

Cirolana cranchi Leach
(Figs 1–3)

Cirolana cranchii Leach, 1818 : 347; Gosse, 1855 : 134, Fig. 230; Hesse, 1866 : 257; Bate & Westwood, 1867 : 296, Fig. 5; Delages, 1881 : 156; Chevreux 1884 : 519; Koehler, 1886 : 25, 61; Bonnier, 1887 : 134; Heape, 1888 : 176; Robertson, 1888 : 76; Hansen, 1890 : 341, Pl. 3, figs 3–3i; 1905 : 350, Pl. 33. fig 3a; Stebbing, 1893 : 343; 1906 : 275; Norman, 1904 : 438; 1907 : 362; Norman & Scott, 1906 : 40, Pl. 4; Monod, 1923 : 14; 1930 : 137, 145, Figs 2, 5B; 1976 : 151; Larwood, 1940 : 33; Barrett & Yonge, 1958 : 99, Fig. 59; Crothers, 1966 : 58; Naylor, 1972 : 28, Fig. 9A–C; Ryland & Nelson-Smith, 1975 : 252; Kussakin, 1979 : 191, Figs 71, 72; Bruce, 1981 : 949.
Nelocira swainsonii Leach, 1818 : 347; Desmarest, 1825 : 302, Pl. 48, fig. 2.
Eurydice swainsonii: Milne-Edwards, 1840 : 236.
Conilera grampoides Gourrett, 1891 : 11, Pl. 1, fig. 7, Pl. 3, figs 4–11.
Cirolana cranchi: Marine Biological Association, 1931 : 183; 1957 : 195; Ellis, 1981 : 123.
Cirolana borealis: Clarke, 1971 : 103 (Non *Natatolana borealis* (Lilljeborg)).
Part *Cirolana cranchii,* Nordenstam, 1946 : 3, Figs 1–5. [More than one species is involved in Nordenstam's description.]
Non *Cirolana cranchii,* Barnard, 1920 : 346; 1940 : 392, 49, 499, Fig. 66; Kensley, 1978 : 65, Fig. 27B, C.[= *Cirolana vicina* Barnard, 1914].

TYPE. The holotype is held by the British Museum (Natural History).

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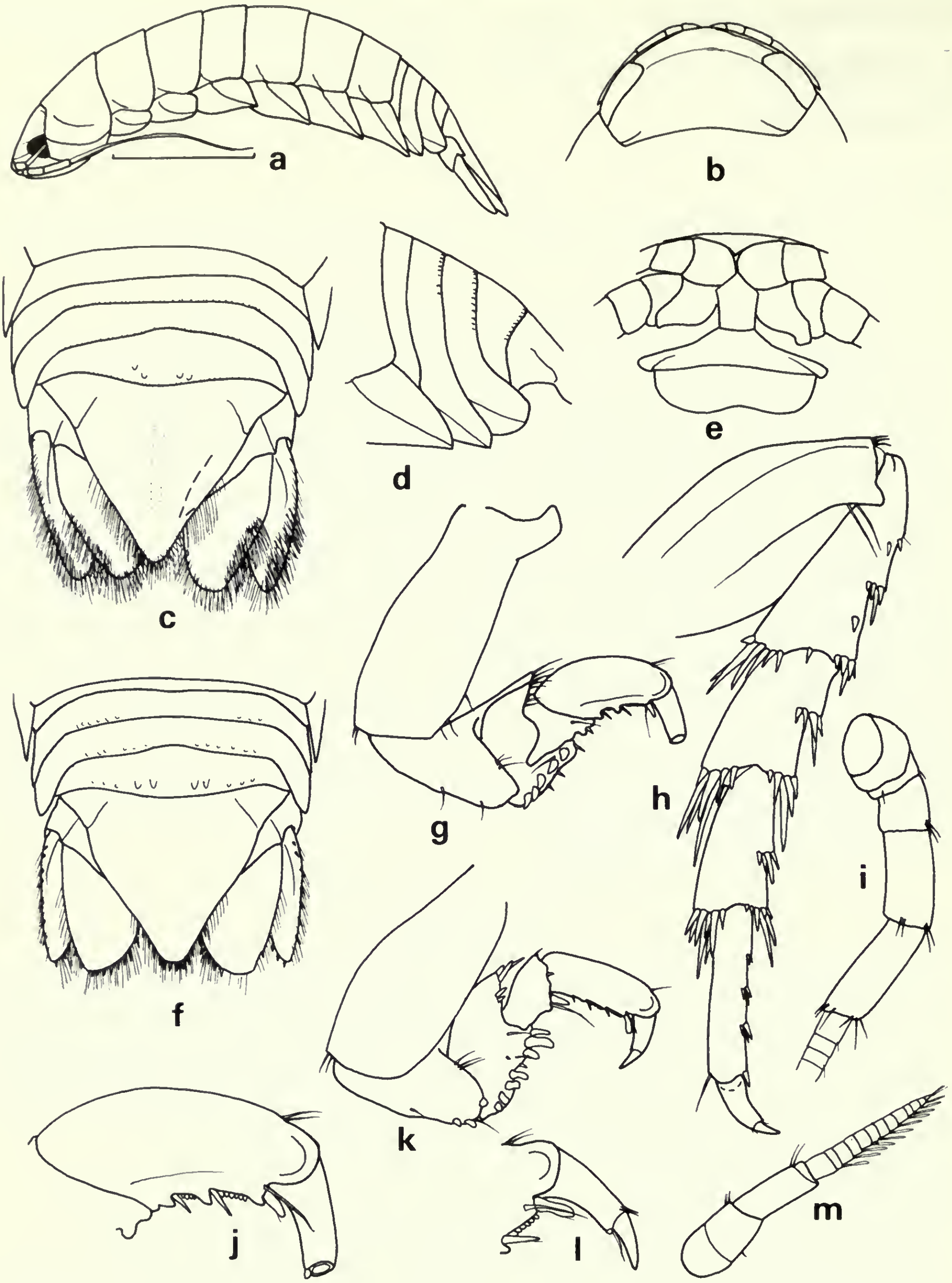

Fig. 1 *Cirolana cranchi:* (a)–(e), ♂ 17·0 mm, Polperro; (f) ♀ 13·3 mm, Polperro; remainder, ♂ 14·0 mm. Plymouth. (a) lateral view; (b) cephalon, dorsal view; (c) pleon and pleotelson, dorsal view; (d) pleon, lateral view; (e) clypeal region; (f) pleon and pleotelson; (g) pereopod 1; (h) pereopod 7; (i) antennal peduncle; (j) pereopod 1, propodus; (k) pereopod 2; (l) pereopod 2, dactylus; (m) antennule. Scale line represents 4·5 mm.

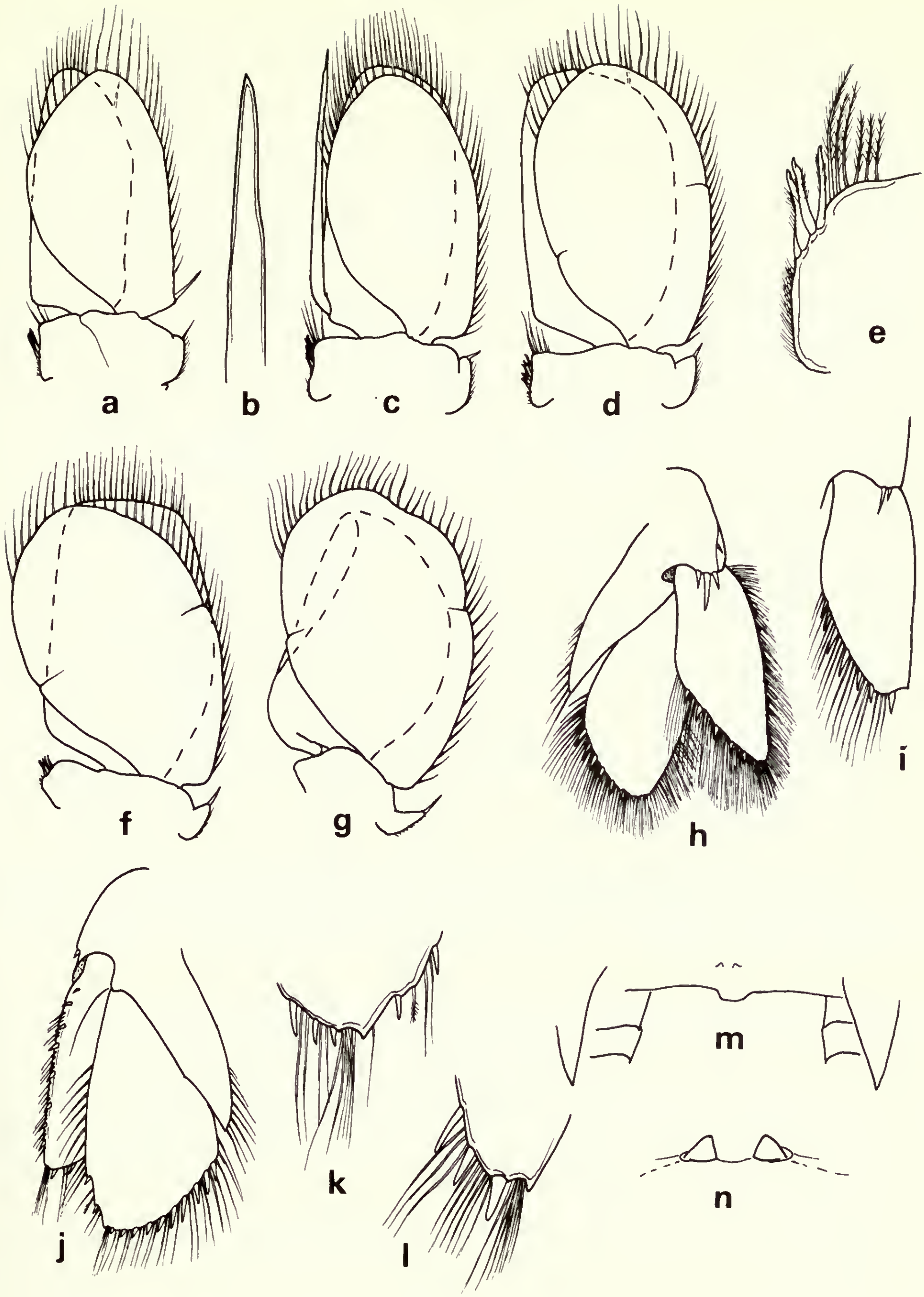

Fig. 2 *Cirolana cranchi:* all figs ♂ 14·0 mm except (i)–(l) ♀ 13·3 mm. (a) pleopod 1; (b) appendix masculina, apex; (c) pleopod 2; (d) pleopod 3; (e) pleopod 2, medial margin of peduncle; (f) pleopod 4; (g) pleopod 5; (h) uropod, ventral view; (i) uropodal exopod, ventral view; (j) uropod, dorsal view; (k) uropodal endopod, apex; (l) uropodal exopod, apex; (m) sternite 7; (n) penes.

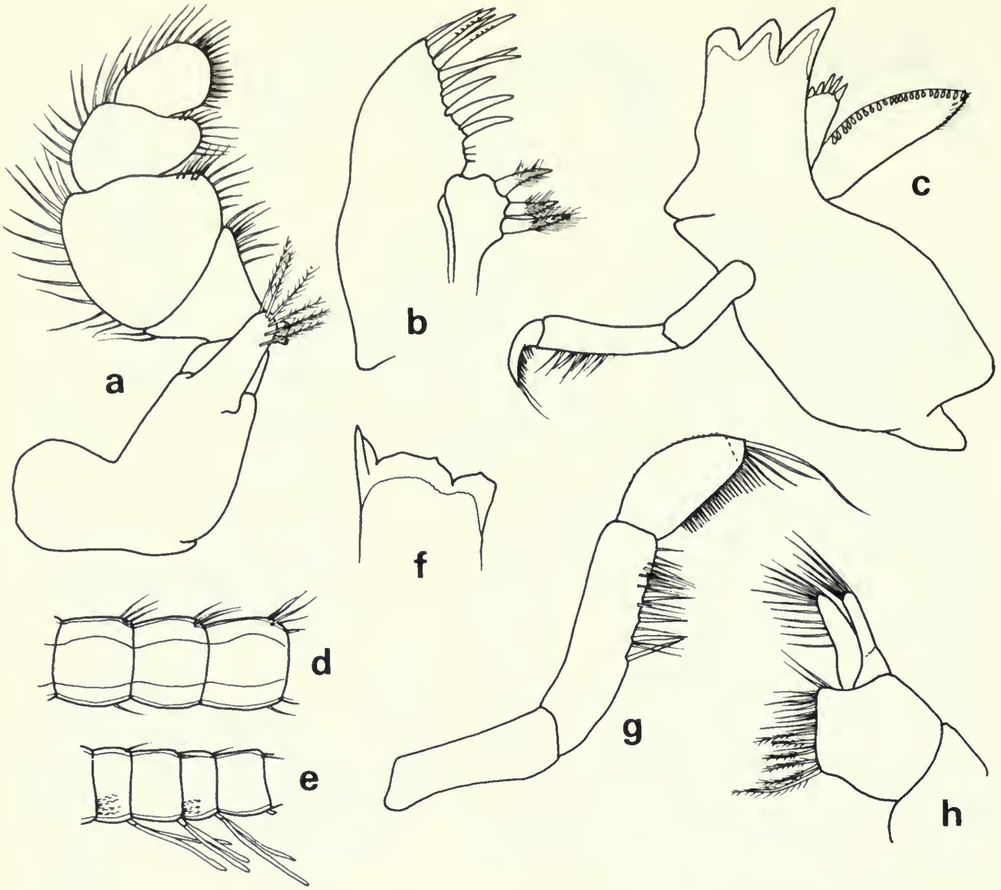

Fig. 3 *Cirolana cranchi:* all figs from ♂ 14·0 mm. (a) maxilliped; (b) maxillule; (c) right mandible; (d) antenna, flagellar articles 9–11; (e) antennule, flagellar articles 4–7; (f) left mandible, incisor; (g) mandibular palp; (h) maxilla.

TYPE LOCALITY. Leach (1818) gives 'Grande Bretagne' as the source of his specimens. Ellis (1981) records the locality as Falmouth, Cornwall.

MATERIAL. 2♂ (17·0, 13·3 mm), Polperro, Cornwall. Coll. A. M. Norman. BM(NH) Reg 1911. 11. 8 : 7840-49. 2♂(14·0, 9·5 mm) ♀ (12·6 mm), Plymouth, Devon. Coll. A. M. Norman. BM(NH) Reg 1911. 11. 8 : 7828–30. ♂ (17·2 mm), 2 ♀ (13·0, 13·5 mm), Torquay, Devon. Coll. A. M. Norman. BM(NH) Reg 1911. 11. 8: 7831–33. These specimens form part of those reported on by Norman (1904).

DESCRIPTION OF MALE. Body about 2·75–3 times longer than wide. Cephalon without rostral process, interocular carina on anterior margin, dorsal interocular furrow extending from the dorsal medial margin of each eye; posterior margin of cephalon with groove on each side indicating presence of maxillipedal somite. Pereonite 1 longest, with 2 horizontal furrows on each side; pereonites 2–7 approximately subequal in length; coxal plates each with distinct carina, posterior margins of coxae 5–7 straight, projecting beyond posterior margin of segment. Pleonite 1 entirely concealed by pereonite 7; pleonite 3 with posterolateral margins moderately produced, those of pleonite 4 rounded; dorsal surfaces of pleonites with posterior margins minutely crenulate, pleonite 5 with additional small tubercles. Pleotelson slightly more than 0·66 as long as greatest width, lateral margins sinuate, converging to narrowly rounded apex; posterior margins densely setose, with about 21 spines; dorsal surface flat except for two oblique anterolateral ridges.

Antennule peduncle triarticulate, articles 1 and 2 appearing fused, although suture evident; peduncular article 3 equal in length to combined lengths of articles 1 and 2; flagellum extends to posterior margin of eye. Antenna with peduncular articles 1 and 2 short, peduncular article 3 about half as long as 4, which in turn is half as long as 5; flagellum composed of about 38 articles, extends to pereonite 4.

Frontal lamina pentagonal, apex not overlapped by rostral process, lateral margins slightly concave, diverging slightly, anterior margins straight; about 0·5 times as long as greatest width. Clypeus about 5·75 times wider than long. Mandibles with asymetrical incisors, that of right mandible with 3 distinctly formed subequal cusps, that of left mandible with posterior cusp prominent, central cusp broad and shallow; molar process with about 25 teeth, inferior distal margin setose, lacina mobilis with about 7 spines; mandibular palp with terminal article curved ventrolaterally, lateral margins with numerous stiff setae. Maxillule with about 10 stout spines on gnathal surface of exopod, 3 robust plumose setae on proximal half of medial margin. Maxilliped with continuous marginal setae on palp articles 3–5, marginal setae on distal margins only of palp article 2; endite with 3 terminal and 3 lateral plumose setae, and with 2 coupling hooks.

Pereopod 1 with slender spines at posterior distal angle of basis; ischium with 2 setae on posterior margin and 3 setae at anterior distal angle; merus with about 6 setae at anterior distal angle, posterior margin with 3 acute spines and 5 tubercular submarginal spines; carpus with a single spine on posterior margin, set within a conspicuous indentation; propodus with 2 acute spines on palm, each spine set distally to tooth like projection, third robust spine opposes dactylus; margin of propodus minutely denticulate between spines. Pereopods 2 and 3 similar, pereopod 2 with 3 acute spines at anterior distal angle of ischium, 2 blunt spines at posterior distal angle, and third spine on the distal lateral margin; merus with 5 spines at anterior distal angle, posterior margin bisinuate, with 8 stout spines; carpus with a single stout spine and single seta on posterior distal angle, spine present on lateral distal margin; propodus with 3 spines on palm, fourth spine opposing the dactylus; dactylus with weakly developed but distinct secondary unguis, as in all pereopods. Pereopods 5–7 similar, pereopod 4 intermediate in form between anterior (1–3) and posterior (5–7) pereopods. Pereopod 7 with about 2 setae and anterior distal angles of propodus, otherwise without setae; distal angles of ischium, merus and carpus each with a group of spines; posterior margin of ischium and produs with further 3 groups of 1–4 spines; posterior margins of merus and carpus with further group of spines; propodus has spine opposing dactylus.

Penes set together on posterior of sternite 7, separated from each other by about 0·05 the width of the sternite; penes are not robust, but rather lamellar flaps of cuticle which originate posteriorly, and project anteriorly, lying against sternite.

Pleopods 3–5 with exopods with partial suture. Peduncles of pleopods 1–5 becoming progressively shorter towards posterior, peduncle of pleopod 1 twice as wide as long, peduncle of pleopod 4 3·5 times as wide as long; lateral distal angles each with a single spine, medial margin 3–5 coupling hooks on pleopods 1–4, pleopod 5 without coupling hooks. Pleopod 1 with rami subequal in length, endopod with margins parallel, exopod with spine at proximal lateral angle. Pleopod 2 with endopod fractionally longer than exopod; appendix masculina arises basally, extends beyond endopod by 0·1 of its length, narrows smoothly to an acute apex.

Uropods extend distinctly beyond apex of pleotelson. Exopod slightly shorter than endopod, lateral margin smoothly convex, with continuous marginal setae and about 9 spines, distal half of lateral margin with dense mass of setae extending on to dorsal surface; medial margin with distinct angle half way along its length, distal half with 6 spines and dense mass of marginal setae; apex not bifid. Endopod with lateral margin angled at about 0.33 of the way along its length, proximal 0·66 densely setose, setae extending onto dorsal surface; medial margin convex with dense marginal setae and about 8 spines; apex not bifid.

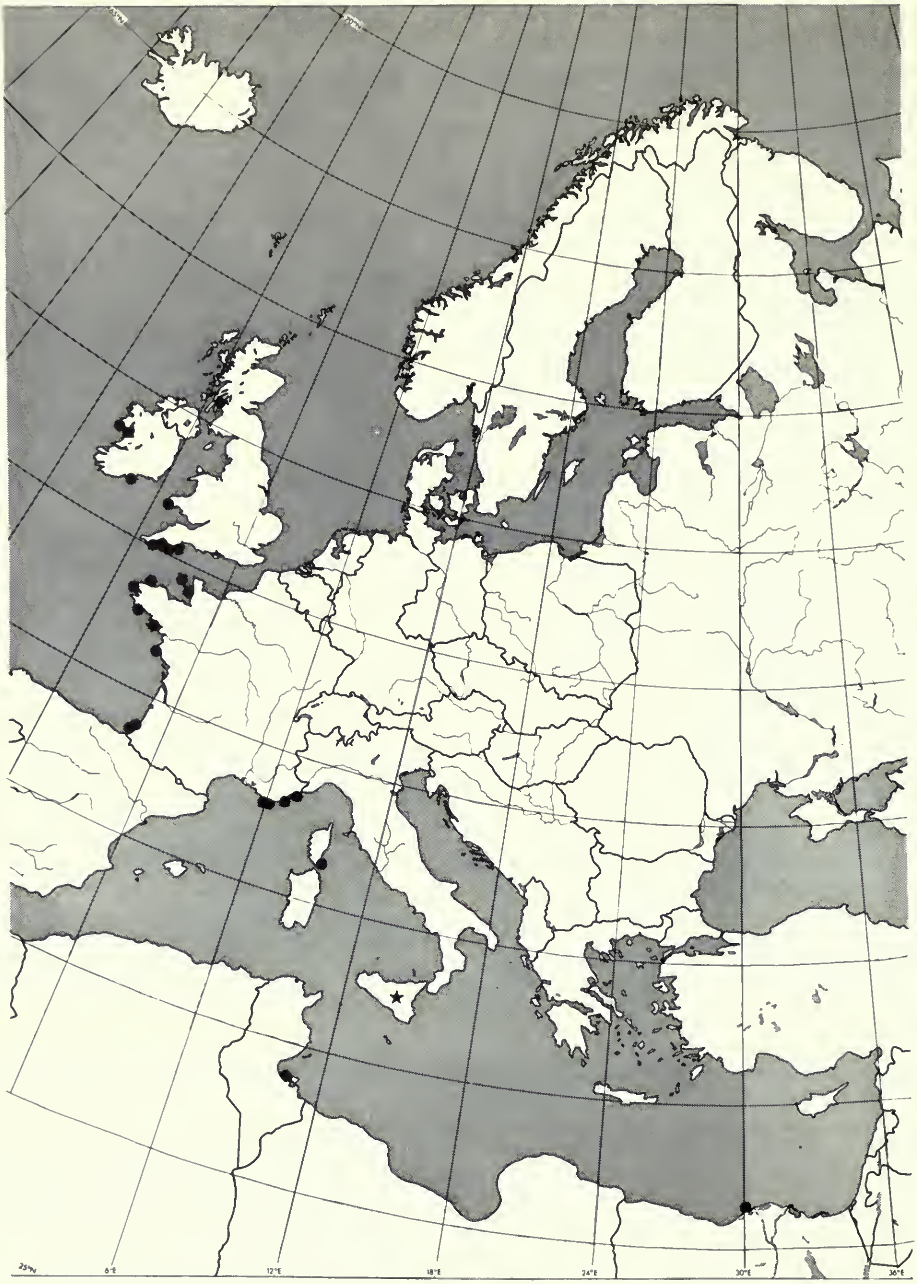

Fig. 4 Map showing the distribution of *C. cranchi*. *Type locality of *Nelocira swainsonii* Leach, 1818 given as Sicily.

FEMALE. The only differences from the male are in the shape of the pleotelson which is wider, in the shape of the uropods which are not angled, and the lack of the dense setae on the pleotelson and uropods.

DEVELOPMENT. Young males are similar to females, and the characteristic shape and setation of the uropods of large males is acquired gradually. One female has oostegites, and measured 13·3 mm.

VARIATION. From the specimens examined, it would appear that the minute crenulations on the pleonites are not visible in large males. The presence and distribution of tubercles on the dorsal surface of the pleonites is erratic.

SIZE. Hansen (1905) records the largest specimen as a female of 18.0 mm. Museum material had adult males from 9·0–19·1 mm, females ranged from 9·6–19·2 mm.

COLOUR. In alcohol, all a pale tan. Barrett and Yonge (1958) describe the colour as 'very pale grey, minutely dotted on first three segments; rear edge of first seven segments marked by transverse line'.

REMARKS. The shape and setation of the pleotelson and uropods are unique, and immediately separate *Cirolana cranchi* from all other species of *Cirolana*. Other characters useful in separation include the shape of the frontal lamina, the shape of the posterolateral margins of the pleonites, the length and shape of appendix masculina, the shape of the endopod of pleopod 1, and the form of the penes.

Cirolana cranchi can be separated from *C. parva* by the lack of a rostral point, by not having the frontal lamina overlapped by a rostral projection, and the very different shape, setation and spination of the pleotelson and uropods.

DISTRIBUTION. Reliably recorded only from the eastern North Atlantic and Mediterranean. These records are summarized here together with new records from the collections of the British Museum. Fig. 4 illustrates the present distribution of *Cirolana cranchi.*

Firth of Clyde: Cumbrae (Bate & Westwood, 1867); Fairland Point, Cumbrae (Robertson, 1888).
Galway Bay, Eire: Spiddal (Ryland and Nelson-Smith, 1975); near Galway (Naylor, 1972); North Sound (Clark, 1971, as *Cirolana borealis).*
Nymphe Bank: Ballycotton, County Cork, Eire (BM(NH) Collections).
St George's Channel: Dale, Pembroke (Crothers, 1966).
English Channel: Falmouth (BM(NH), holotype); Gwyllyn Vase, Falmouth (Stebbing, 1906); Polperro, Cornwall; Torquay (Norman, 1904); Plymouth, outside breakwater (Bate & Westwood, 1867); Batten, Mewstone Ledge, Tinside and Stoke Point, Plymouth (Marine Biological Association, 1957); Knapp Buoy, Plymouth (Heape, 1888); Torbay (BM(NH) collections); Anstis Cove, near Torquay (Stebbing, 1893); Jersey (Koehler, 1886); off St Sampson's Harbour, Guernsey (Norman, 1907); Roscoff (Delages, 1881).
Bay of Biscay: Minou, Brittany (Hesse, 1866); Concarneau (Bonnier, 1887); Grands-Carneaux and east of Belle-Isle, Croisic (Chevreux, 1884); Le Croisic; Belle Isle; Ile d'Yeu; Guethery, near Biarritz (Hansen, 1905); Capbreton (Norman, 1904).
Mediterranean: Toulon; Cannes; Porto Vecchio, Corsica; Gabes, Tunis (Hansen, 1905); Rade d'Hyeres (BM(NH) collections); Brusq, Var (Gourret, 1891, as *Conilera grampoides);* Villefranche (Hansen, 1890); Monaco (Monod, 1923); Sicily (Leach, 1818, as *Nelocira swainsonii*); Alexandria (Larwood, 1940).

Discussion

Leach (1818) recorded *Cirolana cranchi,* the second species of what was to become the family Cirolanidae. The species then received little attention up to the revision of the family by Hansen (1890). In that publication and a later one Hansen (1905) reviewed all previous records. Records published since Hansen's two publications have basically contributed little towards an increased knowledge of the species. Monod (1930) figured the pleopods, and Kussakin (1979) gave new figures for the antenna, pereopods 1 and 7 and the male second pleopod, his other figures being taken from Hansen (1890). From this it can be seen that although the figures given by Hansen (1890) are of a high standard, no modern description has been given.

As a consequence of the lack of detailed description *Cirolana cranchi* has become confused with *Cirolana parva.* The initiator of this confusion was Stebbing (1917) who considered *C. cranchi* and *C. parva* as likely to be synonymous. This opinion was later followed by Nordenstam (1946) who went to some length to demonstrate that the two species were one. Unfortunately, he chose to do this by illustrating pereopod characteristics, the one character likely to lead to the conclusion to which he came. Pereopods in the genus *Cirolana* (sens. str. Bruce, 1981) vary very little between species. Monod (1976) entered the argument in describing a *Cirolana* sp. from Togo, West Africa. In this paper Monod reviewed the arguments of previous authors, and discussed Hansen's (1890) diagnoses. Monod came to the conclusion that the West African species could be assigned neither to *cranchi* nor to *parva* and nor could they be said not to belong to those species. In effect, that *parva* and *cranchi* are not separable.

When reviewing this debate, the most surprising aspect is that the problem existed at all. Hansen's (1890) figures clearly separate the two species. The differences in frontal lamina shape, pleotelson and uropods, presence and absence of rostral process are all clearly shown. Hansen also states that in *parva* the uropod apices are bifid, and in *cranchi* entire. It also seems remarkable that no author encountering this problem has sought to redescribe the species involved as a solution. Comparison of the figures, description and remarks given here to those of Bruce & Bowman (1982) show that *Cirolana cranchi* and *Cirolana parva* are two readily separable species.

As there has been some confusion over the species included under the synonymies of *Cirolana cranchi,* the most important of these are now listed and discussed.

Cirolana swainsonii: Miers, 1881. Examination of Miers' specimens shows that they represent a species related to, but distinct from *cranchi* that has yet to be described.
Cirolana vicina Barnard, 1914. This species is very similar to *C. cranchi* and should be redescribed before final judgement on its status is passed. From Barnard's (1914) description it differs in having 'sub-bifid' uropod apices, and lacks the dense mass of setae on the uropods.
Cirolana cranchii var. *australiense* Hale, 1925. This species is in no way a race or variety of *C. cranchi.* It differs in the shape of the frontal lamina, pleotelson and posterolateral margin of pleonites 2–4, and has a distinct rostral process.
Cirolana cranchii: Nordenstam, 1946. Nordenstam's material came from Europe, South Africa and the Pacific, and consisted of *C. cranchi., C. vicina* and a species of unknown identity from the Pacific.
Cirolana australiense Naylor, 1961. This species is closest to the variety described by Hale (1925), but may be a distinct species. Naylor's specimens were from the Chatham Islands, New Zealand.
Cirolana sp.: Monod, 1976. Monod figures two '*Cirolana* sp', one from Togo, and one from the Congo. One of these is *Cirolana chaloti* Bouvier, 1901 (Bruce, in press), and the other species may well be new. Monod's (1931) record of *C. cranchi* may be of one of these species.

In conclusion, it should be emphasized that in identifying or describing species related to *C. parva* and *C. cranchi* particular care and attention should be given to details of the frontal lamina, the relative position and shape of the penes, the shape of the posterolateral margins of pleonites 2–4, the first and second pleopods of the male, and most importantly details of the pleotelson and uropods.

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Valettietta, a new genus of deep-sea amphipod (Gammaridea: Lysianassidae) with descriptions of two new species from the North Atlantic Ocean

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Introduction

Within the gammaridean family Lysianassidae the combination of a strongly toothed mandibular incisor and unspecialized gnathopods is shared by only 4 genera, *Valettia* Stebbing, 1888, *Alicella* Chevreux, 1899, *Valettiopsis* Holmes, 1908 and *Valettiella* Griffiths, 1977. Each is monotypic with the exception of *Valettiopsis* which comprises 4 species, *dentata* Holmes, 1908, *macrodactyla* Chevreux, 1909, *anacantha* Birstein & Vinogradov, 1963 and *multidentata* Barnard, 1961. Barnard (1969) included one other genus, *Onesimoides* Stebbing, 1888, in his key to lysianassids having a toothed incisor, but there is some doubt as to the true nature of the mandibular margin. Stebbing (1888), in his description of *O. carinatus* says '. . . cutting edge . . . seemingly of the usual form . . .'. In *O. cavimanus,* the mandible has '. . . bord tranchant presque simple, renforcé à chacun de ses angles par des bourrelets de chitine. . . .' (Pirlot, 1933), while in *O. chelatus* the cutting edge is simple (Pirlot, 1933).

Those genera with a strongly dentate incisor share a broadly similar facies and can be regarded as forming a natural group, with the omission of *Valettia coheres* which has a quite different morphology, especially in the structure of the mouthparts. The choice of names for these genera has turned out to be rather unfortunate since the genus name *Valettia* was used as the stem term for the later taxa *Valettiopsis* and *Valettiella* with which it does not have close affinity.

Valettiopsis and its allies live at moderate to great ocean depths and have as a consequence been infrequently recorded. In fact, all six species were first described from unique types, and only *dentata* and *macrodactyla* have since been redescribed from additional material (Barnard, 1967; Chevreux, 1935). Recent deep-water collections from the North Atlantic made during cruises of RRS *Discovery* and RRS *Challenger* have produced 5 mature individuals of this rare lysianassid group, one belonging to *Valettiopsis macrodactyla,* the other 4 representing two species new to science. The combination of characters shared by the two new species puts them close to *Valettiopsis,* but with sufficient disparity in the configuration of the coxal plates, pereopodal bases, and mandibular palp armature to justify the erection of a new genus for which we propose the name *Valettietta* gen. nov. One existing species of *Valettiopsis,* namely *V. anacantha* from the Philippine Trench in the Pacific, is transferred to the new genus.

Systematics

Family LYSIANASSIDAE

Genus *VALETTIOPSIS* Holmes, 1908

DIAGNOSIS. Body robust, compressed, pleosome well developed; urosome segment 1 with

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large, acute, mid-dorsal tooth, segment 3 broad and dorsally flattened with lateral margins raised. Antenna 1 and 2 elongate, slender, subequal length, peduncle articles 2-3 of antenna 1 compressed, flagellum article 1 conjoint, accessory flagellum well developed, multiarticulate. Upper lip weakly notched; lower lip without inner lobes, mandibular lobes elongate. Mandible having robust incisor, strong spine row interspersed with plumose setae, and large triturative molar; palp attached level with molar, article 2 elongate with only distomarginal setae. Maxilla 1 inner plate densely setose along entire inner margin, palp robust, 2-articulate. Maxilla 2 inner and outer plates subequal length, inner plate with dense mediodistal and facial setae. Maxilliped basic, outer plate with short inner marginal spines grading distally to robust elongate spines. Coxal plate 1 much shorter than 2 and partly concealed; plate 4 with only shallow posterior emargination. Coxal plate 5 anterior lobe deeper than posterior lobe. Epimeral plate 2 distal angle with tooth. Gnathopods 1 and 2 subchelate; gnathopod 1 palm transverse. Pereopod 7 basis expanded, lacking posterodistal lobe. Uropods biramous, lanceolate, spinose; uropod 3 outer ramus 2-articulate. Telson deeply cleft, each lobe with several large apical spines. Branchial lobes bearing small accessory lobe at the base.

TYPE SPECIES. *Valettiopsis dentata* Holmes, 1908 (original designation).

REMARKS. Three of the *Valettiopsis* species names *(dentata, anacantha, multidentata)* have been corrected to give the epithets feminine terminations. Holmes (1908) derived the name *Valettiopsis '. . . from Valettia*, a genus of Amphipods, and ὄψis, appearance'. Greek nouns ending in *ops,* genitive *opsis,* are feminine and adjectival specific names must agree in gender with their genus name (International Code of Zoological Nomenclature, Articles 11 (g) (i) (1), 34 (b)).

Valettiopsis macrodactyla Chevreux

Valettiopsis macrodactyla Chevreux, 1909 p. 1, figs 1–2; 1935 p. 8, pl. 2, fig. 1.

MATERIAL EXAMINED. 1♂ Bay of Biscay abyssal plain, about 47° 15′–28′ N 8° 9′–46′ W; 4300 metres; collected by Dr A. G. Macdonald during RRS *Challenger* cruise, October, 1978, using baited trap. BM(NH) reg. no. 1979 : 8 : 1.

DESCRIPTION. Figs 1a–h; 2a–h; 3a–k. Length 17 mm. Body robust, compressed, pleosome segments strongly developed; urosome segment 1 with prominent dorsal tooth, upper margin of tooth weakly sinous, apex acute. Epimeral plates 2–3 (Fig. 2h) with posterodistal tooth. Head (Fig. 1b) with triangular lateral lobe apically produced and with sinuous lower margin; postantennal sinus very shallow; eyes absent. Antenna 1 elongate, peduncle article 1 slender, longer than 2–3 combined; flagellum 30-articulate; accessory flagellum 9-articulate, reaching slightly beyond end of basal conjoint article of flagellum; conjoint article of flagellum equal to length of peduncle, densely setose on inner surface; remaining flagellar articles sparsely setose. Antenna 2 longer than 1, peduncle article 5 slightly longer and more slender than 4, flagellum 40-articulate, proximal flagellar articles with erect setules on inner margin. Upper lip (Fig. 2a) rounded with minute apical notch. Lower lip (Fig. 2b) outer lobes elongate, robustly spinulose on inner distal margin; inner lobes absent, mandibular lobes well developed. Right mandible (Fig. 2c, d), incisor robustly 7-dentate, lacinia also strongly toothed, comprising two plates with 7 and 4 teeth; spine row with 11 large spines interspersed with long plumose setae, distal spines dentate; molar strongly triturative; palp robust, article 3 oval with inner distal margin robustly setose, article 2 elongate, inner distal margin with long setae, inner proximal margin naked. Maxilla 1 (Fig. 2e) inner plate with entire inner margin densely setose; palp large, article 2 distal margin with stout short spines and row of submarginal setae. Maxilla 2 (Fig. 2f) inner and outer plates subequal, densely setose, inner plate also with row of facial setae. Maxilliped (Fig. 2g) inner plate with 3 short apical spines; outer plate inner margin bearing row of spines that are short and stout proximally grading to elongate and plumose distally; palp elongate, article 3 with row of strong facial setae, article 4 inner margin bearing 2 short spines.

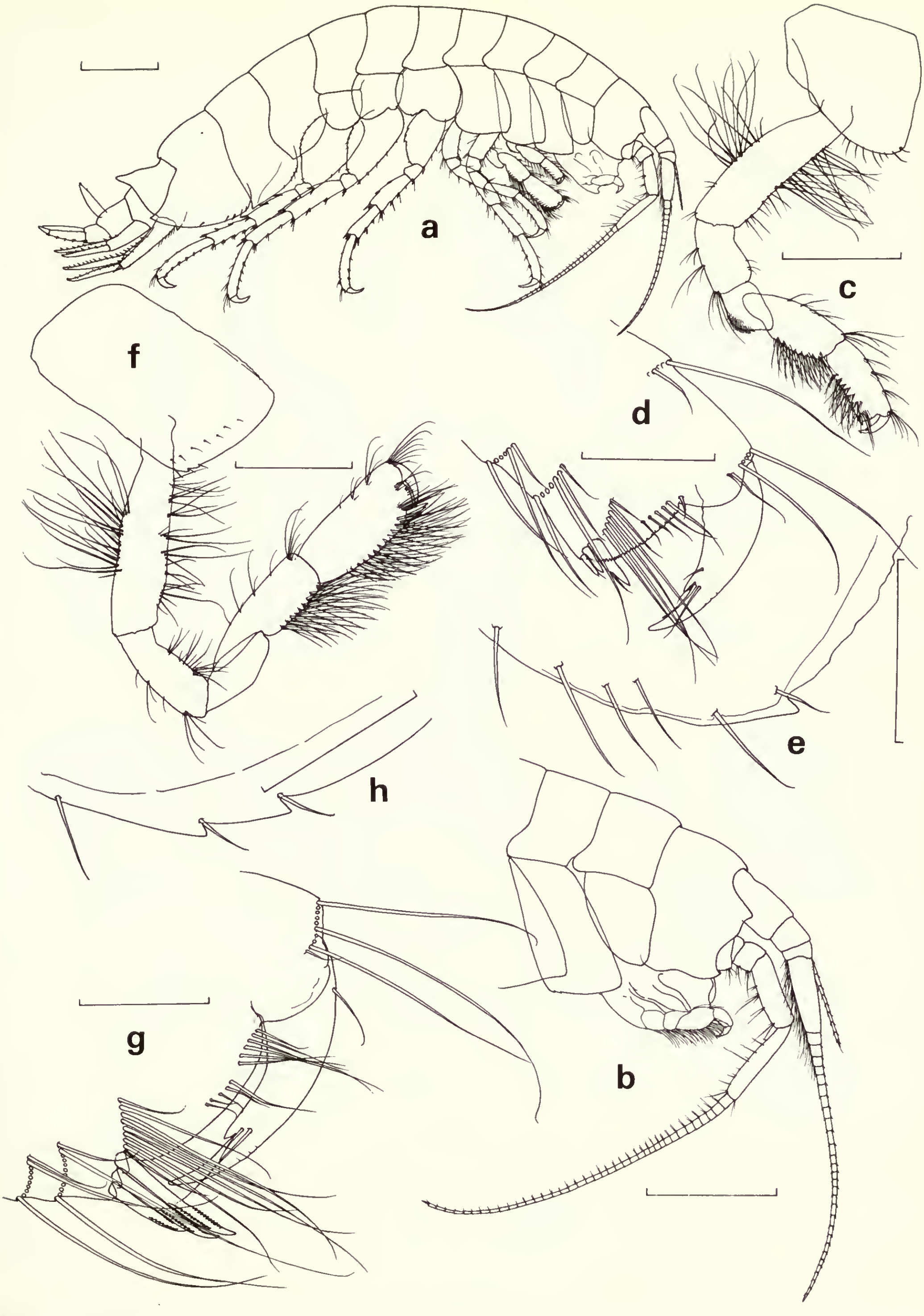

Fig. 1 *Valettiopsis macrodactyla* Chevreux. Male. a, habitus; b, head and antennae; c, gnathopod 1; d, gnathopod 1, palmar region; e, coxal plate 1, anterodistal margin; f, gnathopod 2; g, gnathopod 2, palmar region; h, coxal plate 2, posterodistal margin. Bar scales: a, b, 2·0 mm; c, f, 1·0 mm; d, e, g, h, 0·2 mm.

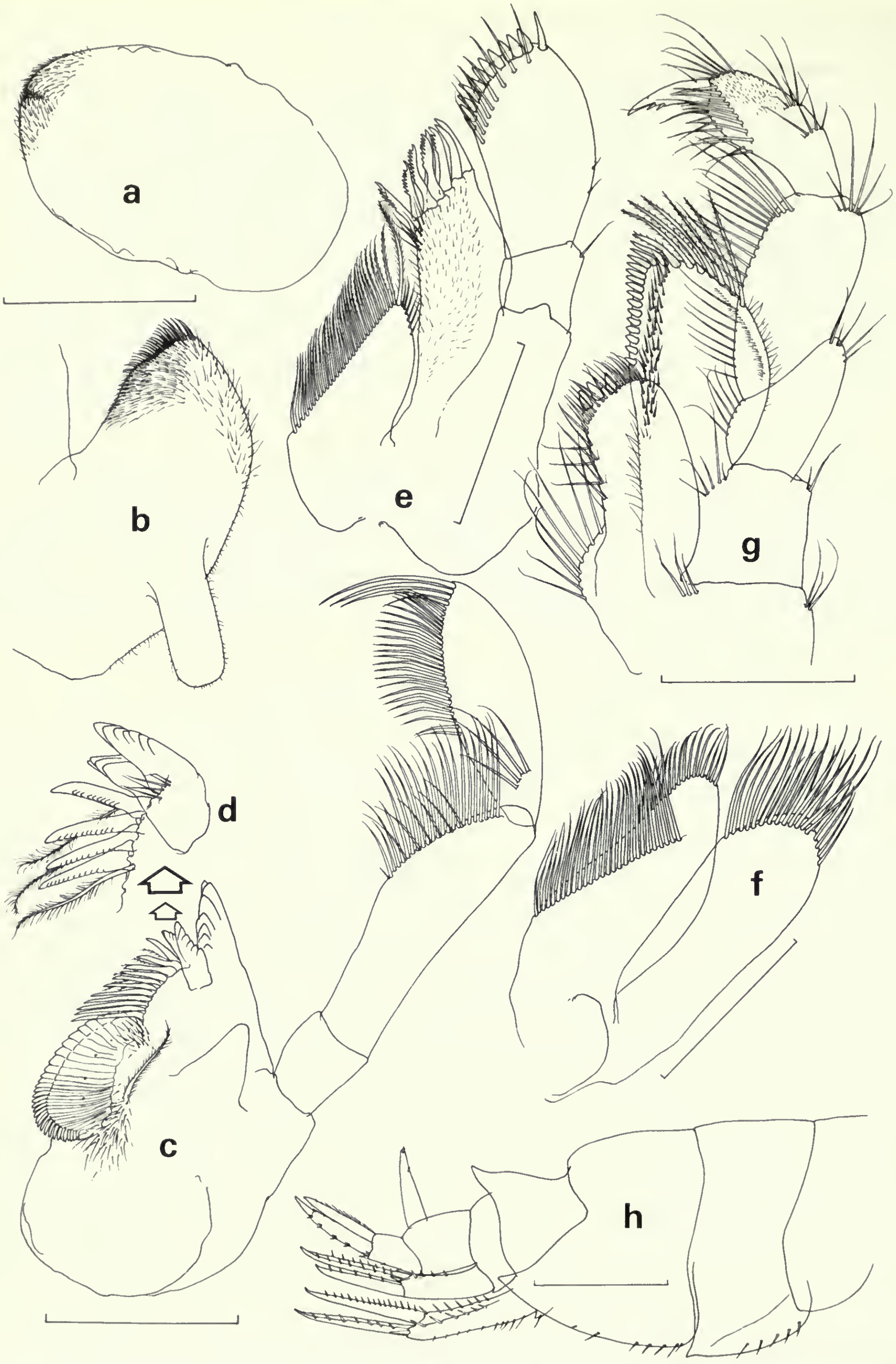

Fig. 2 *Valettiopsis macrodactyla* Chevreux. Male. a, upper lip; b, lower lip; c, right mandible; d, lacinia mobilis and spine row, right mandible; e, maxilla 1; f, maxilla 2; g, maxilliped; h, pleon. Bar scales: a–g, 0·5 mm; h, 2·0 mm.

Gnathopod 1 (Fig. 1c, d) subchelate, coxal plate short, triangular, apically rounded, anterodistal margin with small tooth (Fig. 1e), distal margin setulose; basis with long setae on anterior and posterior margins; ischium elongate; merus short with mat of short setules on posterior margin; carpus little longer than propodus, setose on posterior margin; propodus rectangular, strongly setose, palm transverse (Fig. 1d), delimited by group of stout spines, palmar margin minutely toothed; dactylus short, slightly overlapping palm, inner margin with small tooth. Gnathopod 2 (Fig. 1f, g) subchelate; coxal plate rectangular, posterodistal margin with 2 small teeth (Fig. 1h); basis with many long setae on anterior and posterior margins; ischium elongate; merus small; carpus equal to length of propodus, posterior margin densely setose; propodus robust, densely setose, palm oblique (Fig. 1g) convex, delimited by group of large dentate spines, palmar margin smooth; dactylus stout with small tooth on inner margin. Pereopod 3 (Fig. 3a), coxal plate rectangular, distal margin weakly sinuous, posterodistal angle with 2 small teeth (Fig. 3b); basis curved, merus robust; carpus shorter than propodus. Pereopod 4 (Fig. 3c) similar to 3, except coxal plate with broad shallow posterior emargination, distal margin without tooth. Pereopods 5–7 (Figs 3d, e, f) robust, spinose; basis with tapering posterior lobe, distal angle weakly produced on 5, not produced on 6–7, bearing 1–2 slender submarginal spines, posterior margin weakly serrate, distal margin of basal lobe on pereopod 7 bevelled. Uropods biramous, spinose; uropod 1 (Fig. 3g) rami subequal, inner margins of rami minutely serrate; uropod 2 (Fig. 3h) outer ramus little shorter than inner; uropod 3 (Fig. 3i) distal article of outer ramus about one-third length of proximal article, inner margin of inner ramus setose. Telson (Fig. 3j) elongate triangular, cleft to three-quarters length, inner apical margin rounded, outer apical angle (Fig. 3k) with 4 graduated spines.

DISTRIBUTION. Known only from the North Atlantic in the region of the Azores (Chevreux, 1935) at 1692–1919 m, and from the present Biscay record at 4300 m.

VALETTIETTA gen. nov.

DIAGNOSIS. Body robust, compressed; pleosome well developed; urosome segment 1 with weak dorsal process, segment 3 broad and flattened dorsally with lateral margins raised. Antenna 1 and 2 elongate, slender, about equal length; peduncle articles 2–3 of antenna 1 compressed, flagellum article 1 conjoint, accessory flagellum well developed, multiarticulate. Upper lip weakly notched. Lower lip without inner lobes, mandibular lobes prominent. Mandible with robustly dentate incisor, spine row strong, interspersed with plumose setae, molar large and triturative, palp attached level with molar, article 2 elongate with proximal and distal margin setose. Maxilla 1 inner plate densely setose along entire inner margin, palp robust, 2-articulate. Maxilla 2 inner and outer plates subequal length, inner plate with dense mediodistal and facial setae. Maxilliped basic; outer plate with short stout inner marginal spines grading distally to robust elongate spines. Coxal plates 1–4 forming continuous series; plate 4 with deep posterior emargination. Coxal plate 5 anterior lobe not deeper than posterior lobe. Gnathopod 1 subchelate; palm oblique; gnathopod 2 subchelate or simple. Pereopods 5–7 basis expanded with prolonged rounded posterodistal lobe. Uropods biramous, lanceolate, spinose. Telson triangular, deeply cleft. Branchial lobes with small accessory lobe close to base.

TYPE SPECIES. *Valettietta lobata* sp. nov.

ETYMOLOGY. The affinity of the new genus to *Valettiopsis* is recognized by adding the diminutive ending *–etta* to the common stem. Gender feminine.

Valettietta lobata sp. nov.

MATERIAL EXAMINED. Holotype ♂, Bay of Biscay abyssal plain, about 47°15′–28′N 8°9′–46′W; 4300 metres; collected by Dr A. G. Macdonald during RRS *Challenger* cruise 1980, using baited trap. BM(NH) reg. no. 1982 : 204.

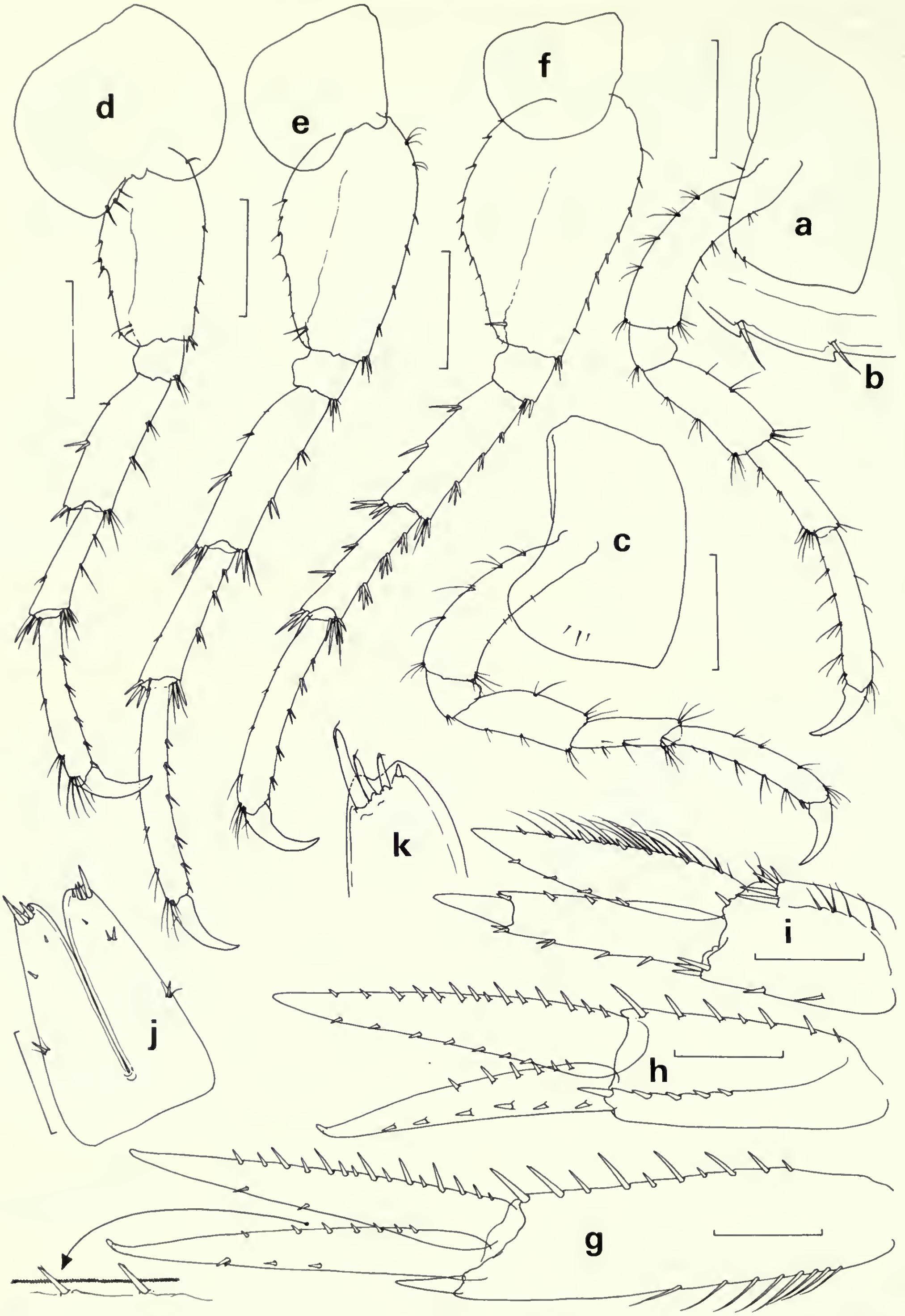

Fig. 3 *Valettiopsis macrodactyla* Chevreux. Male. a, pereopod 3; b, coxal plate 3, posterodistal margin; c, pereopod 4; d, pereopod 5; e, pereopod 6; f, pereopod 7; g, uropod 1; h, uropod 2; i, uropod 3; j, telson; k, apex of telson lobe. Bar scales: a–f, 1·0 mm; g–j, 0·5 mm.

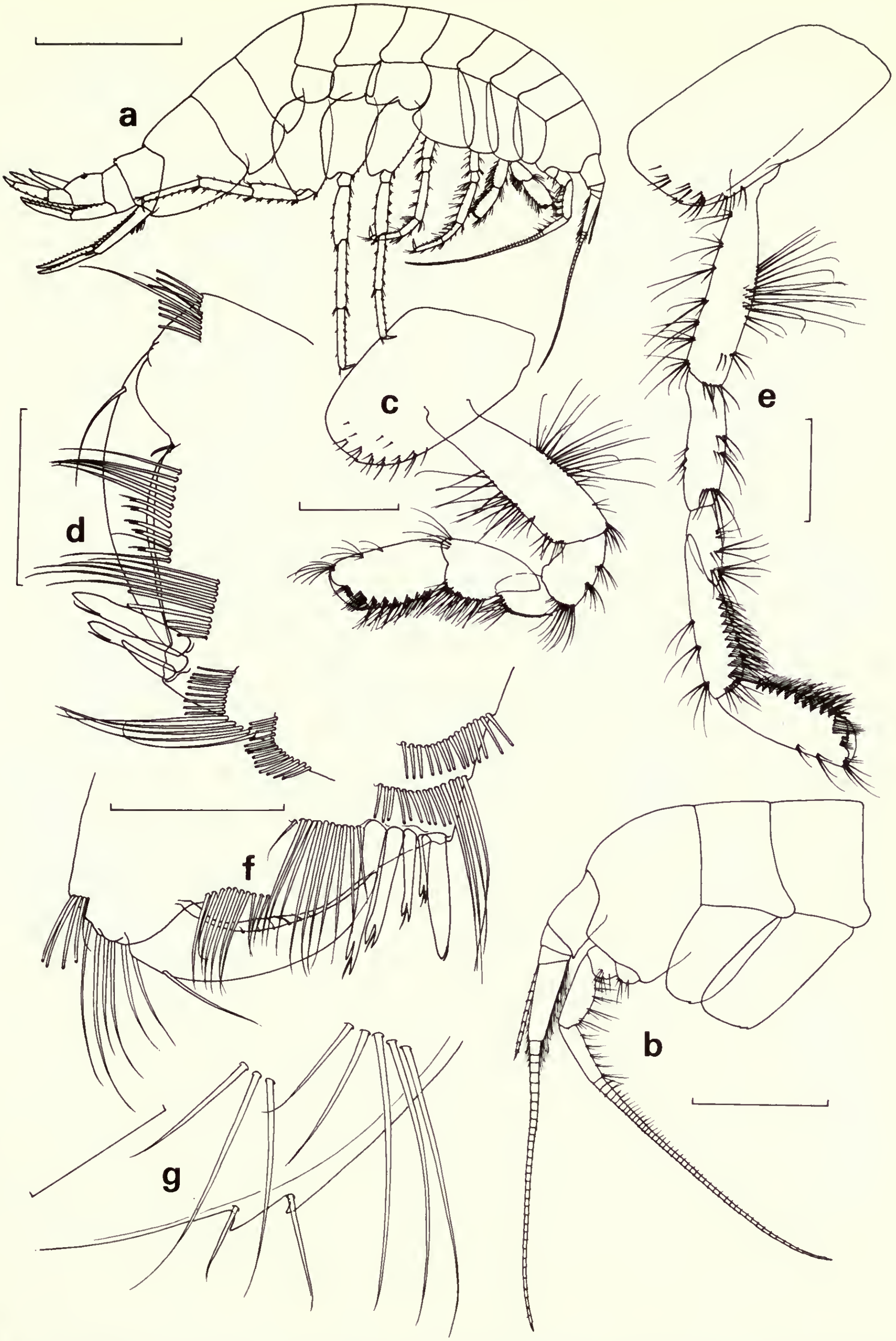

Fig. 4 *Valettietta lobata* sp. nov. Holotype. a, habitus; b, head and antennae; c, gnathopod 1; d, gnathopod 1, palmar region; e, gnathopod 2; f, gnathopod 2, palmar region; g, coxal plate 2, posterodistal margin. Bar scales: a, 5·0 mm; b, 2·0 mm; c, e, 1·0 mm; d, f, g, 0·2 mm.

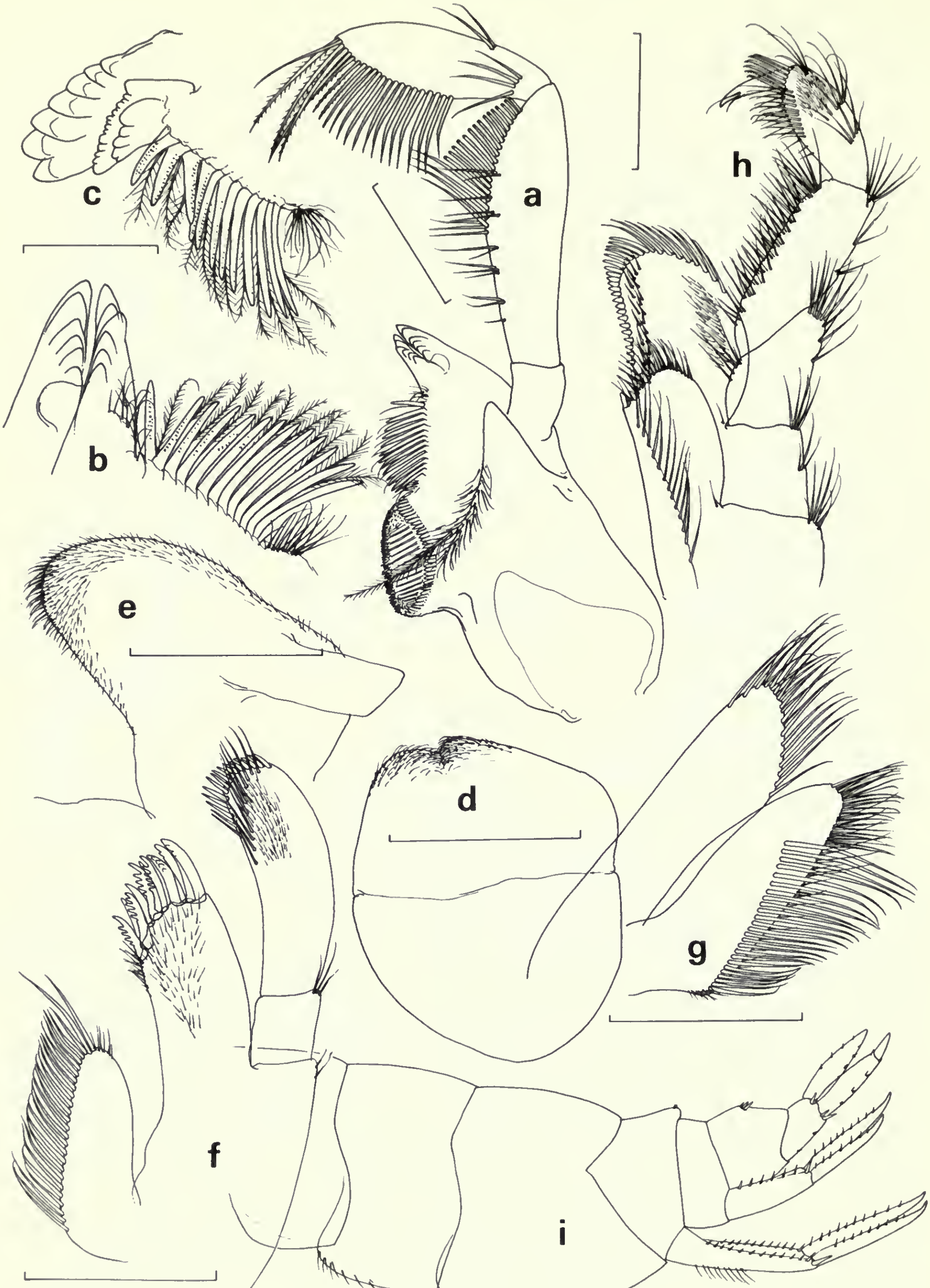

Fig. 5 *Valettietta lobata* sp. nov. Holotype, a, left mandible; b, left mandible, incisor, lacinia and spine row; c, right mandible, incisor, lacinia and spine row; d, upper lip; e, lower lip; f, maxilla 1; g, maxilla 2; h, maxilliped; i, pleon. Bar scales: a, d-h, 0·5 mm; b, c, 0·2 mm; i, 2·0 mm.

Paratype ♂, *Discovery* station 9541 #19, north west of Cape Verde Islands, RMT 1+8 combination net, 18 April 1977, 4040–3970 m (fished 0–20 metres off bottom); 20°19·7′ N 21°51·3′ W–20°18·4′ N 21°40·5′ W. BM(NH) reg. no. 1982 : 205.

ETYMOLOGY. The epithet refers to the expansive posterior lobe of the pereopod basis.

DESCRIPTION. Figs 4a–g; 5a–i; 6a–m. Holotype. Length 21·5 mm. Body robust, compressed, pleosome segments strongly developed; urosome segment 1 with small rounded median knob-like process bearing pair of minute apical spinules. Epimeral plate 2 (Fig. 5i) distal angle quadrate, plate 3 distal angle acute. Head (Fig. 4b) large, lateral lobe triangular, postantennal sinus very shallow; eyes absent. Antenna 1 elongate, peduncle article 1 slender, posterodistal angle with small tooth, articles 2–3 short, flagellum 34-articulate; accessory flagellum 10-articulate, reaching little beyond end of basal conjoint article of flagellum; conjoint article 1 equal to length of peduncle, densely setose on inner surface, remaining flagellar articles sparsely setose. Antenna 2 little longer than 1, peduncle articles 4–5 subequal length, flagellum 48-articulate, proximal articles with erect setules on posterior margin. Upper lip (Fig. 5d) asymmetrically rounded with small apical notch, distal surface minutely setulose. Lower lip (Fig. 5e) outer lobes elongate, robustly spinulose on inner distal margin, inner lobes absent, mandibular lobes elongate. Mandible (Fig. 5a, b, c), left incisor robustly 8-dentate and closely applied to 6-dentate lacinia; right incisor 7-dentate, well spaced from double bladed lacinia bearing numerous small teeth; spine row with 12–13 large spines interspersed with long plumose setae, distal spines dentate; molar strongly triturative; palp robust, article 3 oval with inner margin spinose, article 2 elongate with regular row of long inner distal setae and irregular groups of shorter proximal setae. Maxilla 1 (Fig. 5f) inner plate with entire inner margin densely setose, outer plate with 2 rows (6 and 5) of pectinate spines; palp large, article 2 distal margin with stout spines and row of submarginal setae. Maxilla 2 (Fig. 5g) inner and outer plates subequal, distally setose, inner plate also with row of facial setae. Maxilliped (Fig. 5h) inner plate with 3 short apical spines, outer plate inner margin with row of short stout spines becoming gradually more elongated and plumose distally; palp elongate, article 3 with row of strong facial setae, article 4 inner margin with 2 small teeth. Gnathopod 1 (Fig. 4c, d) subchelate; coxal plate rounded, distal margin with small tooth, inner distal surface with about 8 groups of setae; basis short, anterior and posterior mid-margins with long setae; ischium elongate, setose; merus short, margin with mat of short setules; carpus shorter than propodus and robustly setose; propodus subrectangular, robust, densely setose, palm weakly oblique (Fig. 4d), smooth, delimited by fan-like group of 6 spines (3 on inner face, 3 on outer face); dactylus short, just reaching to end of palm. Gnathopod 2 (Fig. 4e, f) subchelate, longer and more slender than 1; coxal plate subrectangular, posterodistal margin with 2 small teeth (Fig. 4g), inner distal surface with about 6 groups of 2–5 setae; basis slender, anterior and posterior margins setose; ischium elongate; merus small; carpus equal to length of propodus, densely setose; propodus subrectangular, setose, palm weakly oblique (Fig. 4f) convex, delimited by fan-like group of 6 spines; dactylus short, not reaching end of palm; gnathopod 2 with characteristic twist in appendage between basis and merus that reverses the orientation of distal articles. Pereopod 3 (Fig. 6a), coxal plate slender, rectangular, posterodistal angle with 2 small teeth (Fig. 6b); basis curved; merus elongate slender and much longer than carpus; dactylus small, straight. Pereopod 4 (Fig. 6c) similar to 3, except coxal plate with broad moderately deep posterior emargination, posterodistal margin with small notch (Fig. 6d). Pereopods 5–7 (Fig. 6e, f, g), robust, spinulose; basis broadly expanded with large posterodistal lobe that becomes more angular from 5 to 7, posterior margin finely serrate; coxal plate of pereopod 6 with posterior lobe distinctly angular. Uropods biramous; uropod 1 (Fig. 6h) rami subequal, robustly spinose; uropod 2 (Fig. 6i) inner ramus just shorter than outer, spinose, adjacent margins minutely serrate; uropod 3 (Fig. 6j) distal article of outer ramus about one-third length of proximal article, apex with pair of minute inset setules (Fig. 6k). Telson elongate triangular (Fig. 6l), cleft to three-quarters length, inner apical margin acute, outer angle with 2 spines set in groove (Fig. 6m); dorsal surface of telson flattened with lateral margins downturned.

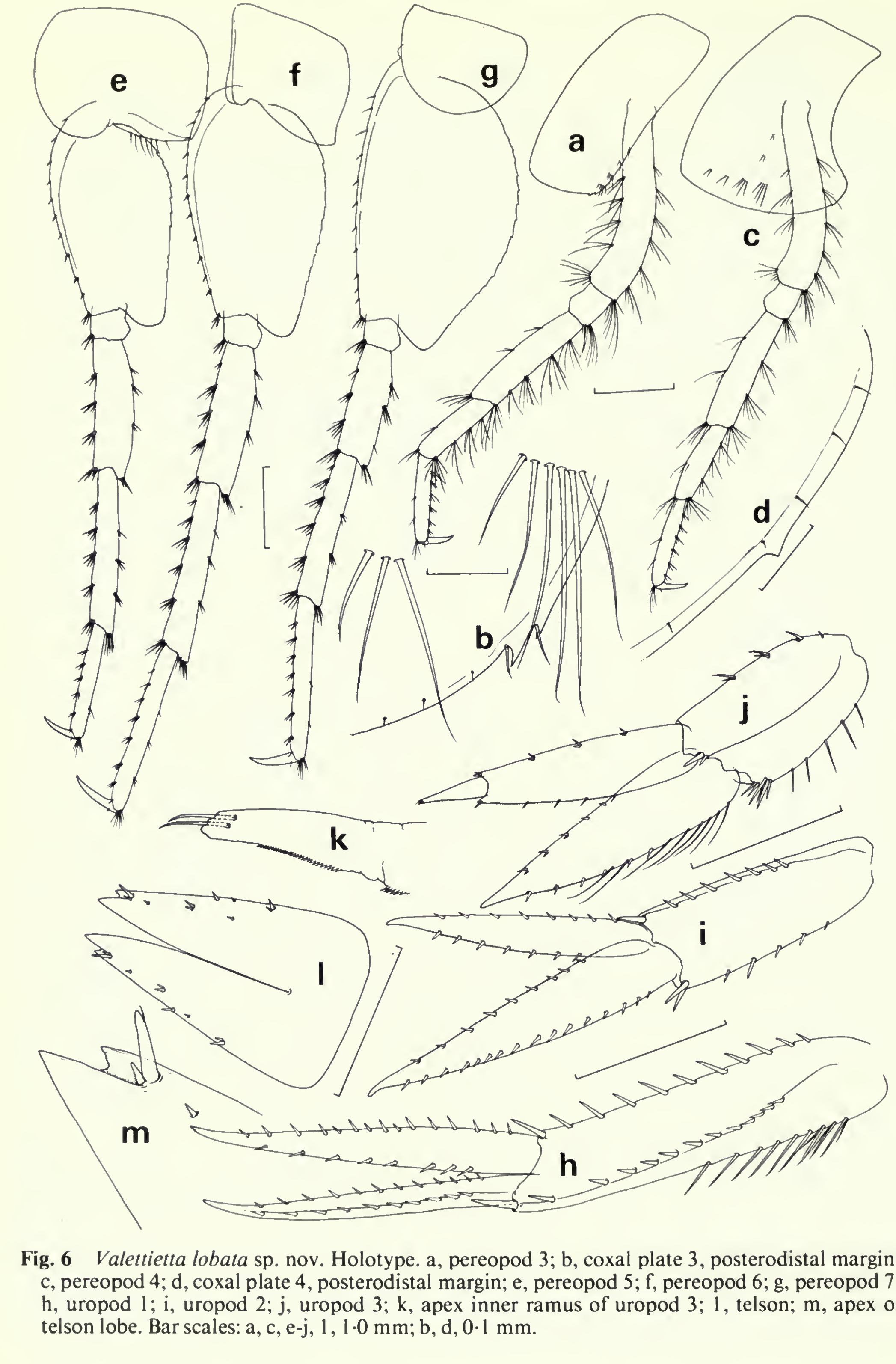

Fig. 6 *Valettietta lobata* sp. nov. Holotype. a, pereopod 3; b, coxal plate 3, posterodistal margin; c, pereopod 4; d, coxal plate 4, posterodistal margin; e, pereopod 5; f, pereopod 6; g, pereopod 7; h, uropod 1; i, uropod 2; j, uropod 3; k, apex inner ramus of uropod 3; l, telson; m, apex of telson lobe. Bar scales: a, c, e-j, l, 1·0 mm; b, d, 0·1 mm.

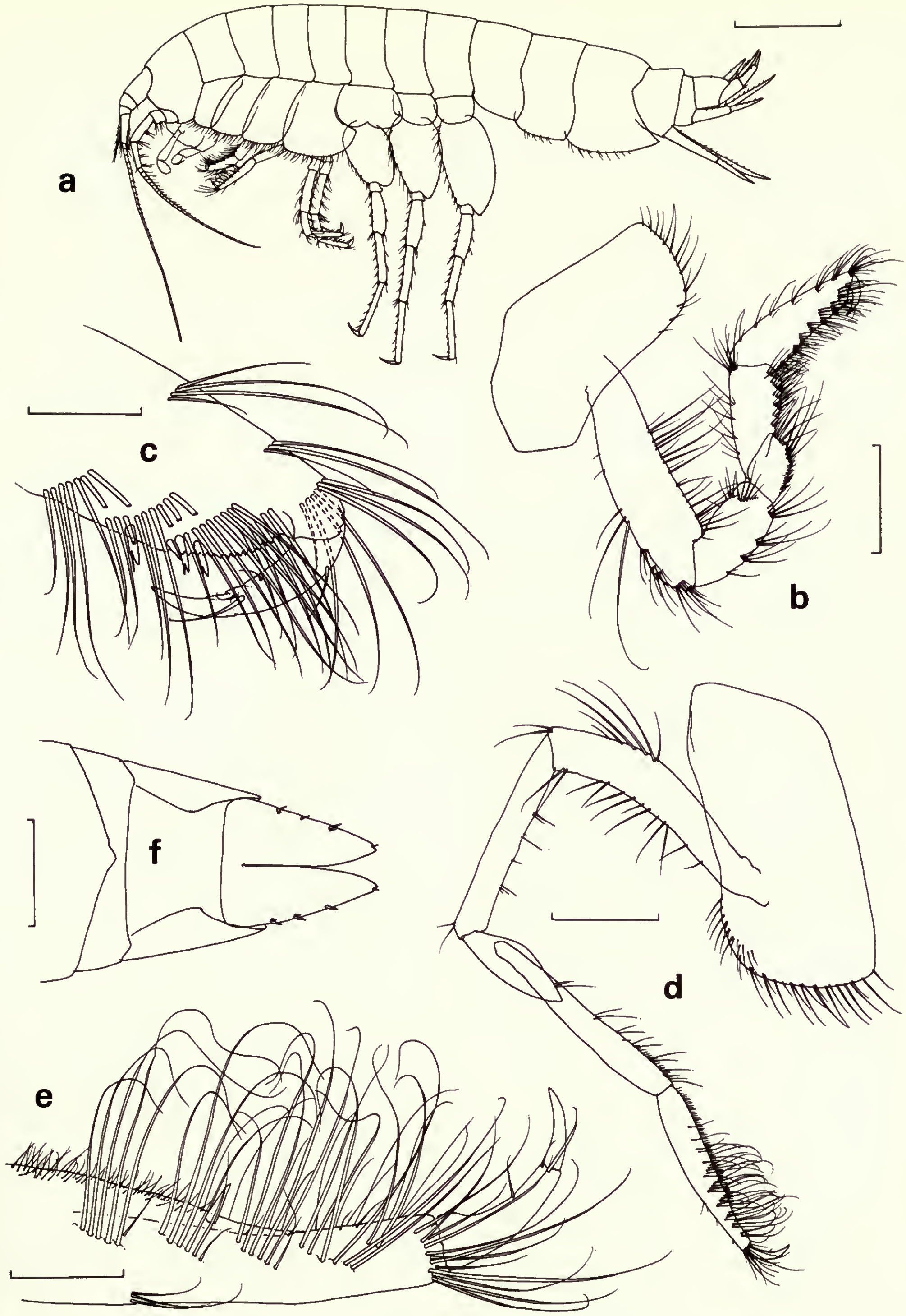

Fig. 7 *Valettietta gracilis* sp. nov. Holotype. a, habitus; b, gnathopod 1; c, gnathopod 1 palmar margin; d, gnathopod 2; e, gnathopod 2 propodus, distal margin; f, urosome, telson. Bar scales: a, 2·0 mm; b, d, f, 0·5 mm; c, e, 0·1 mm.

REMARKS. The paratype male, body length 18 mm, has essentially similar morphology to the holotype; antenna 1 flagellum 25-articulate with especially obvious tooth on peduncle article 1; antenna 2 flagellum 36-articulate bearing calceoli. The structure of the calceolus (Fig. 10) was examined by SEM and was found to approximate to the basic lysianassid form described by Lincoln & Hurley (1981), but with certain unique features that set it apart from all other lysianassid calceoli described to date. These include the 4 broad crescentic plates that form the distal element and the lack of a cuticular pit at the point of origin of the stalk from the flagellar article.

Valettietta gracilis sp. nov.

MATERIAL EXAMINED. Holotype ♂, Bay of Biscay abyssal plain, about 47°15′–28′N 8°9′–46′W; 4300 metres; collected by Dr A. G. Macdonald during RRS *Challenger* cruise 1980, using baited trap. BM(NH) reg. no. 1982 : 206.

Paratype ♂, *Discovery* Station 9541 #19 north west of Cape Verde Islands, RMT 1+8 combination net, 18 April 1977, 4040–3970 m (fished 0–20 m off bottom); 20°19·7′ N 21°51·3′ W–20°18·4′ N 21°40·5′ W. BM(NH) reg. no. 1982 : 207.

ETYMOLOGY. The epithet alludes to the slender condition of the gnathopod 2 propodus.

DESCRIPTION. Figs 7a-f; 8a-h; 9a-h. Holotype. Length 11 mm. Body compressed, pleosome segments well developed; urosome segment 1 with rounded median process. Epimeral plates 1–2 posterodistal angle obtuse (Fig. 8h), plate 3 acutely produced. Head large (Fig. 8a), lateral lobes triangular, apically rounded; postantennal sinus very shallow; eyes absent. Antenna 1 elongate, flagellum 31-articulate, sparsely setose; accessory flagellum 7-articulate, reaching beyond end of basal conjoint article of flagellum; conjoint article equal to length of peduncle article 1, densely setose on inner surface. Antenna 2 little shorter than 1, peduncle articles 4 and 5 subequal length, flagellum 30-articulate, proximal flagellar articles with erect setules on posterior margin. Upper lip asymmetrically rounded with small apical notch, distal surface minutely setulose. Lower lip (Fig. 8b) outer lobes elongate, inner distal margin robustly spinulose, inner lobes absent, mandibular lobes elongate. Mandible (Fig. 8c, d), left incisor strongly 8-dentate and closely applied to 7-dentate lacinia; right incisor 8-dentate, well spaced from 6-dentate lacinia; spine row with 13 large spines interspersed with long plumose setae, distal spines dentate, molar strongly triturative; palp robust, article 1 small, article 2 extremely elongate with regular row of inner distal setae and irregular groups of proximal setae, article 3 oval with robust marginal setae. Maxilla 1 (Fig. 8e, f) inner plate setose along entire inner margin, outer plate bearing two rows of pectinate spines; palp large, article 2 distal margin with stout spines and row of long submarginal setae. Maxilla 2 inner and outer plates subequal, distally setose, inner plate also with row of facial setae. Maxilliped inner plate with 3 short apical spines; outer plate inner margin with row of short stout spines (Fig. 8g) becoming gradually elongate and plumose distally; palp elongate, setose. Gnathopod 1 (Fig. 7b, c) subchelate; coxal plate rectangular, anterior margin angular, distal margin setose; ischium long and setose; merus small, posterior margin with mat of short setules; carpus much shorter than propodus, posterior margin densely setose; propodus elongate, tapering distally, anterior and posterior margins with long setae; palm oblique (Fig. 7c) convex, dentate, delimited by group of short spines; dactylus overlapping palm, inner margin toothed. Gnathopod 2 simple (Fig. 7d, e), coxal plate rectangular, distal margin setose, smooth; basis curved, anterior and posterior margins setose; ischium extremely elongate; merus small; carpus slender, sparsely setose; propodus slender, tapering distally, margin with groups of long setae that curve inwards to form a setal basket, palm absent but propodal margin with solitary spine close to the closing point of the dactylus. Gnathopod 2 with characteristic twist in appendage between basis and merus that reverses the orientation of the distal articles. Pereopod 3 (Fig. 9a) coxal plate rectangular, distal margin setose; basis curved; merus longer than carpus; propodus and carpus subequal length; all articles with long marginal spinules. Pereopod 4 (Fig. 9b) similar to 3, except coxal plate very broad and

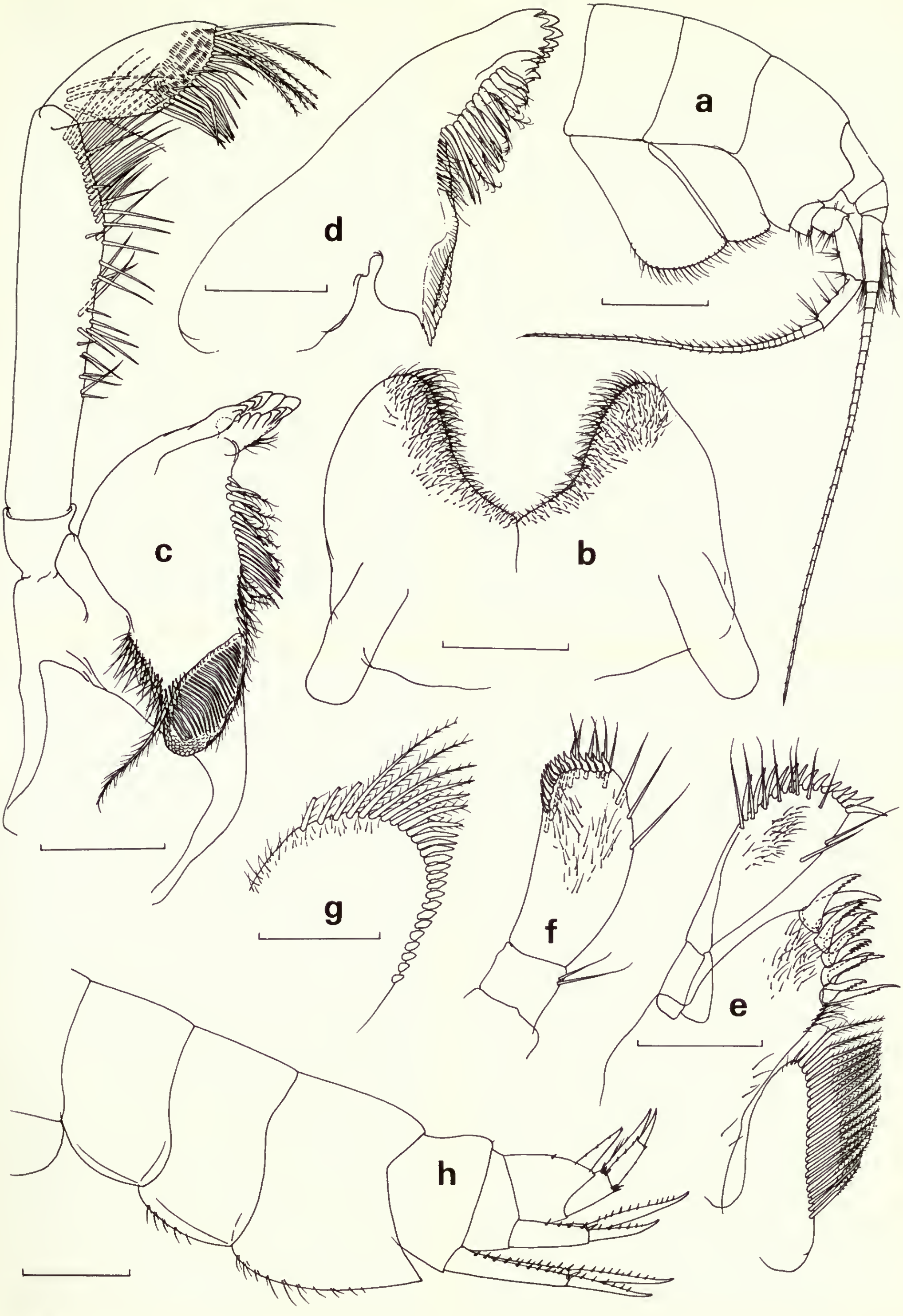

Fig. 8 *Valettietta gracilis* sp. nov. Holotype. a, head and antennae; b, lower lip; c, left mandible; d, right mandible; e, maxilla 1; f, maxilla 1 palp; g, maxilliped outer plate; h, pleon. Bar scales: a, h, 1·0 mm; b-g, 0·2 mm.

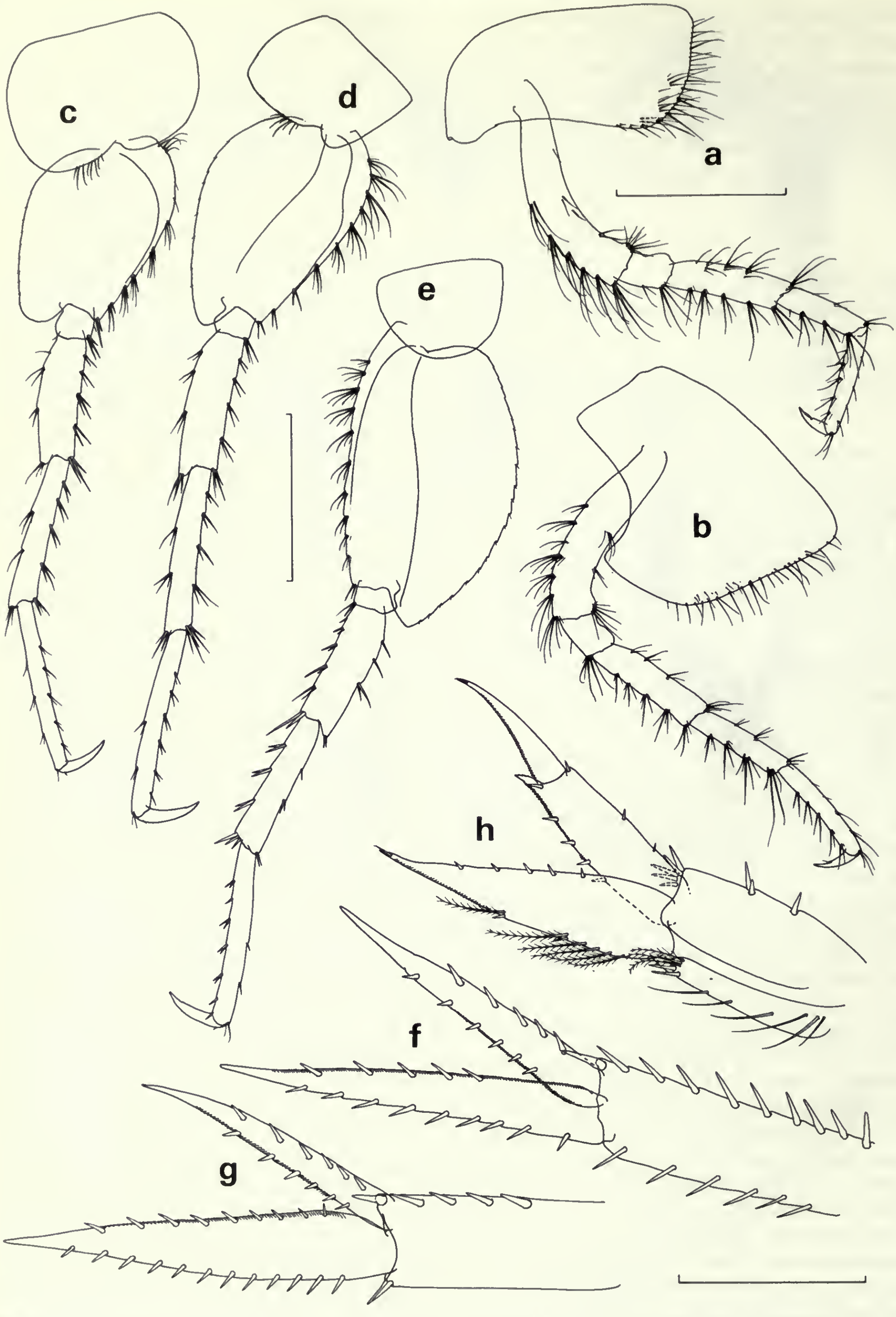

Fig. 9 *Valettietta gracilis* sp. nov. Holotype. a, pereopod 3; b, pereopod 4; c, pereopod 5; d, pereopod 6; e, pereopod 7; f, uropod 1; g, uropod 2; h, uropod 3. Bar scales: a-e, 1·0 mm; f-h, 0·5 mm.

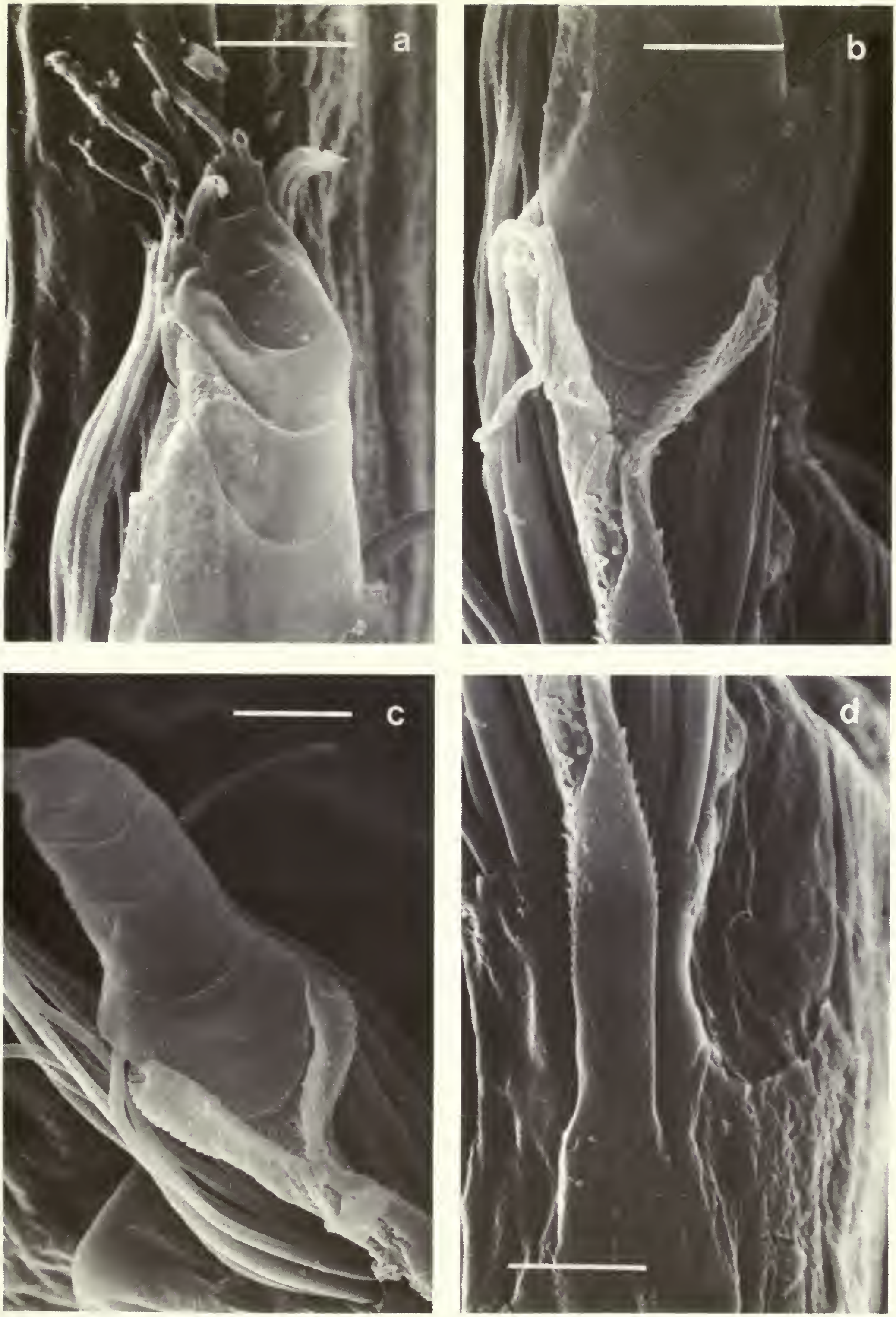

Fig. 10 *Valettietta lobata* sp. nov. Scanning electron micrographs of antennal calceoli; a, b, d sectional photographs of same calceolus, bar scale: 5·0 µm; c, entire calceolus, bar scale 10 µm.

deeply excavate posteriorly, distal margin straight and setose; merus and propodus subequal and longer than carpus. Pereopods 5–7 (Fig. 9c, d, e) robust, spinulose; basis broadly expanded with large posterodistal lobe that becomes more angular from 5 to 7, posterior margin minutely serrate; coxal plate of pereopod 6 with subangular posterior lobe. Uropods biramous; uropod 1 (Fig. 9f) and uropod 2 (Fig. 9g) inner ramus shorter than outer, spinose, adjacent margins minutely serrate; uropod 3 (Fig. 9h) distal article of outer ramus two-thirds length of proximal article, apex of proximal article with triangular tooth, inner margin of inner ramus setose, apex of both rami with inset small setule. Telson (Fig. 7f) triangular, cleft beyond three-quarters length, apex acute with small spinule.

DISCUSSION. The new genus *Valettietta* shares a general appearance and many special features with *Valettiopsis,* but is characterized by the following combination of characters: fully developed coxal plate 1; obtuse epimeral plate 2; produced posterodistal lobes on pereopods 5–7 bases; groups of proximal setae on article 2 of mandibular palp. The species *anacantha* described by Birstein & Vinogradov from a deep-sea station in the Pacific south of the Philippines is transferred to *Valettietta;* it is very close to *gracilis* but can be distinguished by the rounded shape of coxal plate 4 and the presence of a short palm on the propodus of gnathopod 2.

Key to species of *Valettiopsis* and *Valettietta* gen. nov.

1	Coxal plate 1 reduced; urosome with strong acute tooth	***(VALETTIOPSIS)*** 2
	Coxal plate 1 not reduced; urosome lacking strong acute tooth	***(VALETTIETTA* gen. nov.)** 4
2.	Pereon segments 5–7 and pleosome segments 1–3 dorsally dentate	***multidentata***
	Pereon segments 5–7 and pleosome segments 1–3 not dorsally dentate	3
3.	Gnathopod 2 propodus elongate, tapering	***dentata***
	Gnathopod 2 propodus stout, ovo-rectangular	***macrodactyla***
4.	Gnathopod 2 simple, or with very small palm, propodus slender, tapering	5
	Gnathopod 2 subchelate, propodus not slender, ovo-rectangular	***lobata*** sp. nov.
5.	Gnathopod 2 palm oblique, coxal plate 4 distal margin convex	***anacantha***
	Gnathopod 2 lacking palm, coxal plate 4 distal margin straight	***gracilis*** sp. nov.

Valettietta gracilis and *V. anacantha* can be regarded as vicarious species having disjunct distributions, one from the Atlantic Ocean and the other from the Pacific Ocean. The differences separating them, although considered valid at species level, are of a minor nature, and are much less marked than those separating either species from *Valettietta lobata.* Within *Valettiopsis,* the Pacific species *dentata* and the Atlantic *macrodactyla* form a similar species pair. Other Atlantic/Pacific species pairs are known; *Paracallisoma alberti* Chevreux, 1903 and *P. coecum* (Holmes, 1908), and *Crybelocephalus birsteini* Thurston, 1976 and *C. obensis* Birstein & Vinogradov, 1964. The separation of the Atlantic and Pacific elements of these species pairs may have occurred in the geologically recent past. All are meso- to abyssopelagic, and have been found in areas that were contiguous prior to the emergence of the Isthmus of Panama about $3{\cdot}5 \times 10^6$ years B.P. (Keigwin, 1978).

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Three new genera of misophrioid copepods from the near-bottom plankton community in the North Atlantic Ocean

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Introduction

Only three species of the copepod order Misophrioida have been described, *Misophria pallida* Boeck 1864, *Benthomisophria palliata* Sars 1909 and *B. cornuta* Hulsemann & Grice 1964. Despite the small number of species the misophrioids have attracted interest because of the combination of characters that they exhibit, drawn from both the gymnoplean and podoplean lineages within the Copepoda. Attention has recently been drawn to the unique characters that misophrioids display; the possession of a carapace-like posterior extension of the cephalosome, the lack of a nauplius eye in a free living copepod, the distensibility of the gut and the retention of the antennary glands as the functional excretory organs of the adult (Boxshall, 1982). These characters, together with the abbreviated lecithotrophic nauplius phase of the life cycle, can be interpreted collectively as evidence of a bathypelagic origin of the Misophrioida. This interpretation is supported by the discovery of several new misophrioid taxa from the deep North Atlantic Ocean, which was reported at the First International Conference on Copepoda held at Amsterdam in August 1981 (Boxshall, in press).

A total of 37 misophrioids was taken in a single haul fished near the bottom in 3000 m of water to the south west of the Azores. Fourteen of these were *B. cornuta,* 8 were *B. palliata* and 15 represented previously undescribed taxa. Three new genera and species are here described on the basis of 13 of these specimens, the remaining 2 specimens being too badly damaged for description. The new genera are of great phylogenetic significance as they exhibit some very plesiomorphic characters which provide fresh insights on the nature of the appendages of the common ancestor of the Copepoda as a whole. The new records of *B. cornuta* and *B. palliata* further extend their known geographical ranges.

Family MISOPHRIIDAE

Genus *ARCHIMISOPHRIA* nov.

DIAGNOSIS. As for type species.

TYPE SPECIES. *Archimisophria discoveryi* gen. et sp. nov.

Archimisophria discoveryi gen. et sp. nov.

Adult female (Fig. 1A) body length 1·1 to 1·4 mm. Prosome large, apparently 4-segmented but with first free thoracic somite entirely concealed beneath a carapace-like extension from the posterior margin of the maxilliped-bearing somite. Nauplius eye absent. Prominent anteriorly-directed rostrum visible from dorsal aspect, not fused to labrum (Fig. 1B). Cone organs not observed but large mass of glandular tissue present on sides of cephalosome beneath usual location of cone organs. Urosome 6-segmented (Fig. 1C). Surface

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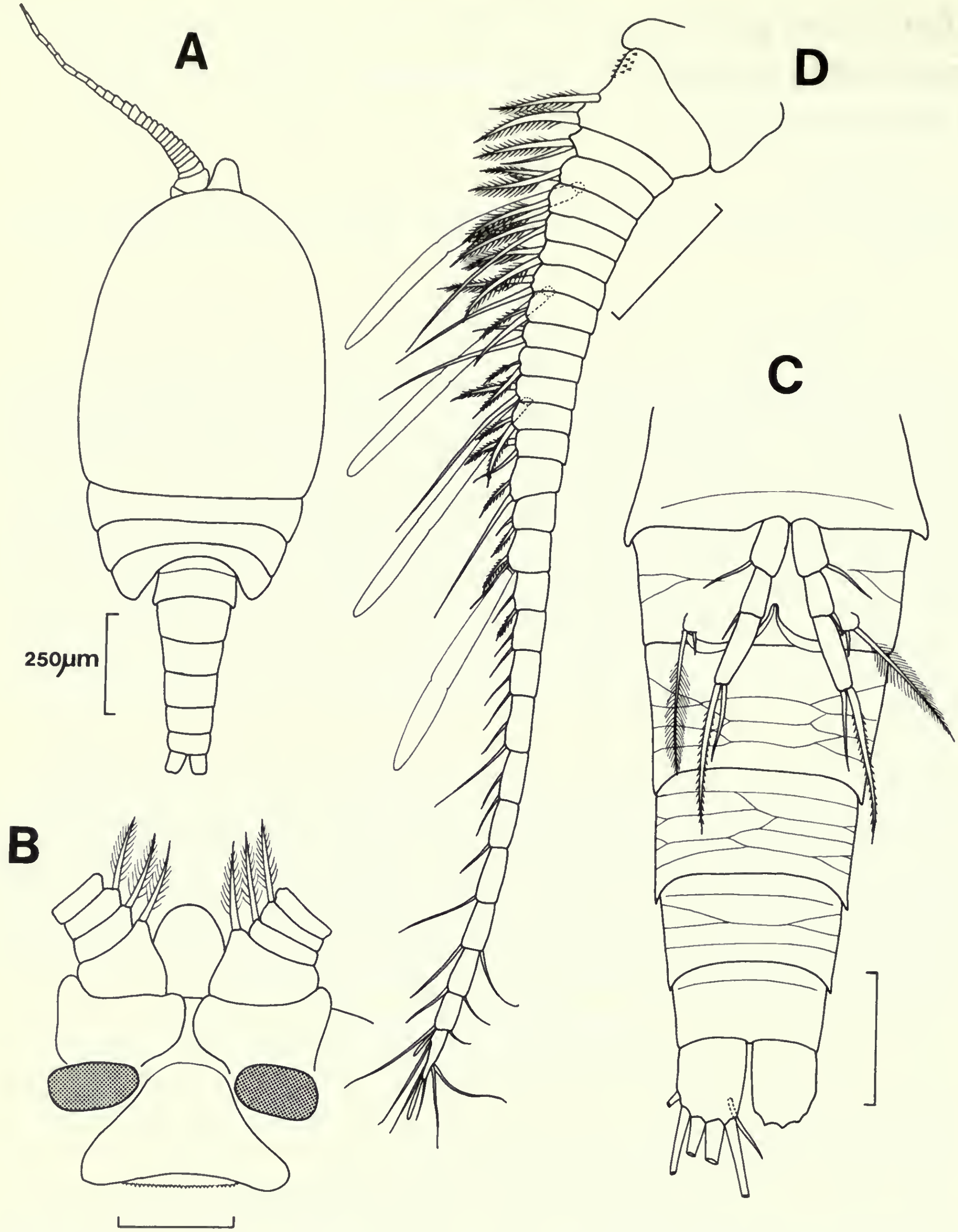

Fig. 1 *Archimisophria discoveryi* gen. et sp. nov. Holotype ♀. A, dorsal view; B, rostrum and labrum, ventral; C, urosome, ventral; D, antennule, dorsal. Scales 100 μm unless otherwise stated.

of prosome and urosome somites 1 to 5 ornamented with a reticulum of epicuticular lamellae. Urosome somite 6 without reticulate markings. Caudal rami longer than wide; armed with 2 long distal margin setae, 2 medium-length distal angle setae, a dorsal seta near the inner margin and a distally located lateral seta.

Antennule (Fig. 1D) 27-segmented, articulating proximally with an expanded area of ventral cephalic surface (Fig. 1B). Armature elements as follows: I–2, II–2, III–2+1 aesthetasc, IV–2, V–2, VI–2, VII–2+1 aesthetasc, VIII–2, IX–2, X–2, XI–2+1 aesthetasc, XII–2, XIII–2, XIV–2, XV–2, XVI–2+1 aesthetasc, XVII–2, XVIII–2, XIX–2, XX–2, XXI–2, XXII–1, XXIII–1, XXIV–2, XXV–2, XXVI–2+1 aesthetasc, XXVII–5+1 aesthetasc. First segment also with patch of minute spinules.

Labrum (Fig. 1B) small, posteriorly directed, not fused with rostrum, with a posterior row of marginal denticles.

Antenna (Fig. 2A), basis lacking inner distal seta; endopod 3-segmented, exopod 8-segmented. Endopod segment 1 apparently unarmed; segment 2 with 4 unequal unilaterally plumose setae at inner distal angle; segment 3 with 6 long subequal unilaterally plumose setae along distal margin and with several transverse rows of spinules. Exopod segment 1 with a short naked seta at inner distal angle; segments 2 and 3 unarmed; segment 4 with a long plumose seta at inner distal angle; segment 5 with 2 long plumose setae on inner margin; segments 6 and 7 small, unarmed; segment 8 with 3 long unilaterally plumose setae on distal margin and areas of spinules subapically.

Mandible (Fig. 2B) with well developed gnathobase bearing distally 2 multicusped blades, 5 strong spines and an extensive fringe of pinnules. Mandibular palp comprising basis, 2-segmented endopod and 4-segmented exopod. Basis armed with a naked seta at inner distal angle. Endopod segment 1 with a short unilaterally plumose seta at inner distal angle; segment 2 with 8 unequal plumose setae along distal margin. Exopod segment 1 unarmed; segments 2 and 3 each with 1 long seta at inner distal angle; segment 4 with 3 similar unilaterally plumose setae and a short naked seta.

Maxillule (Fig. 2C), gnathobase with 14 distal elements; endite 1 with 1 spiniform and 3 setiform armature elements, endite 2 with 3 spiniform elements. Outer lobe rudimentary, represented by 6 plumose setae on outer surface of segment. Maxillulary palp biramous with 2-segmented endopod and 1-segmented exopod. Endopod segment 1 with 3 unequal armature elements at inner distal angle; segment 2 with a long and a short seta proximally on inner surface and an apical armature of 3 long unilaterally plumose setae, 1 long and 2 short naked setae. Exopod with a proximal fringe of pinnules and 6 plumose setae on inner margin and with 3 long unilaterally plumose setae and a naked seta on distal margin.

Maxilla (Fig. 3A) 6-segmented; segment 1 with 6 plumose setae on proximal endite and 3 on distal endite; segment 2 with 3 similar setae on both proximal and distal endites; segment 3 produced medially into a curved claw armed with 3 naked setae near its base; segments 4 to 6 with a total of 10 setae.

Maxilliped (Fig. 2D) 8-segmented, with a 3-segmented, robust proximal portion and a slender 5-segmented distal portion. Segment 1 with 1 seta on inner surface; segment 2 with 2 medial setae and a row of pinnules along the outer margin; segment 3 with proximal endite bearing 1 strong spine and 3 setae, distal endite with 1 naked seta and a long plumose seta, 2 other setae on inner margin, a plumose seta at inner distal angle and a long row of pinnules along outer margin; segments 4 to 6 with 1, 2 and 1 medial setae respectively, each armed with short spinules; segment 7 with an inner margin spinulate seta and an outer plumose seta on which the pinnules decrease markedly in length towards the apex; segment 8 with 3 similar plumose setae and a naked seta.

Legs 1 to 4 incomplete in holotype ♀ and paratype ♀, assumed to be similar to those described below for a paratype ♂.

Leg 5 (Fig. 1C) uniramous, 3-segmented and positioned midventrally with inner margins almost touching at base. Segment 1 with 1 naked seta at outer distal angle; segment 2 with a short naked seta in same position; segment 3 elongate with 2 unequal distal margin setae, the longer armed with spinules bilaterally.

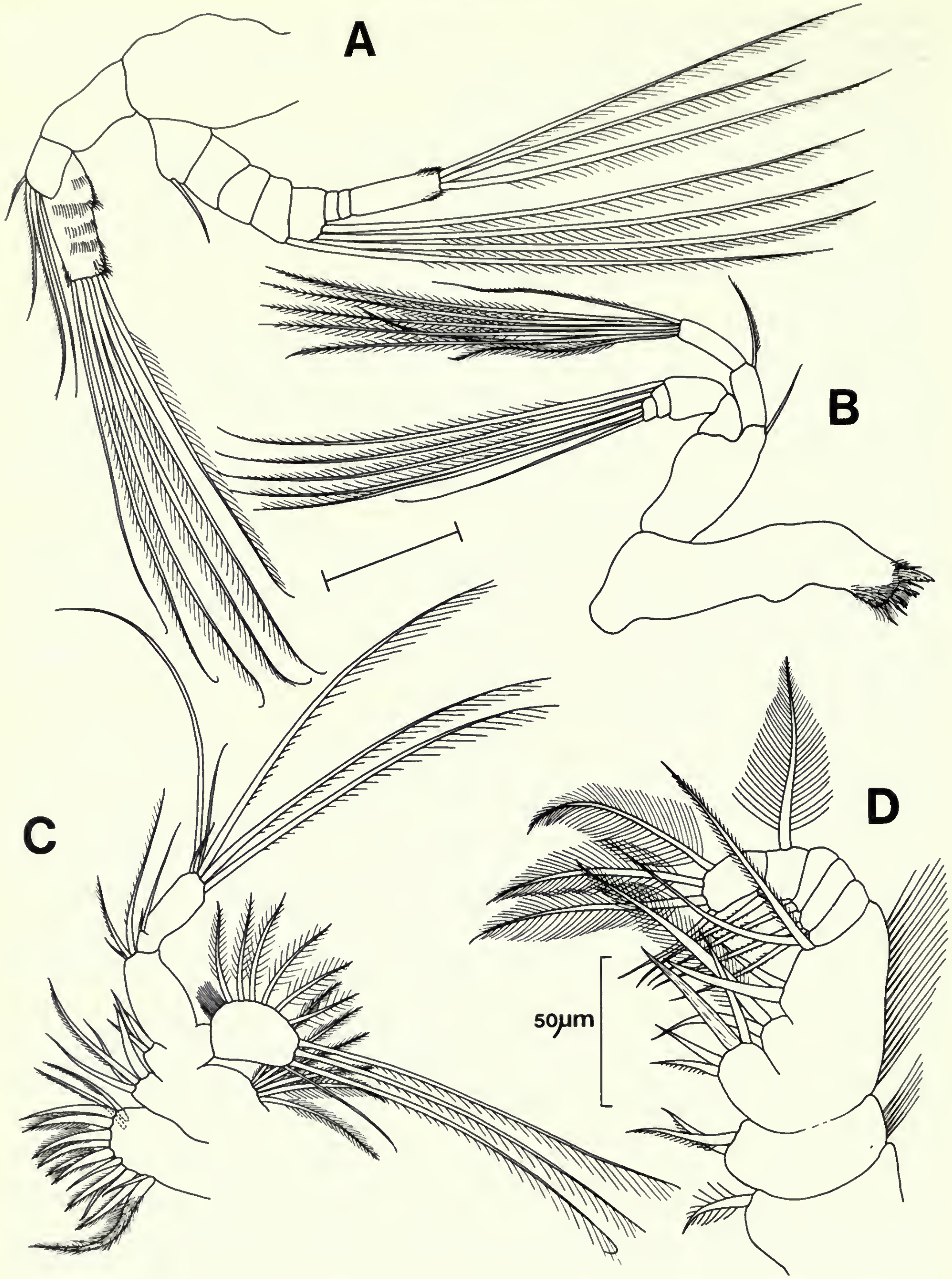

Fig. 2 *A. discoveryi.* A, antenna, anterior; B, mandible, anterior; C, maxillule, posterior; D, maxilliped, posterior. Scales 100 µm unless otherwise stated.

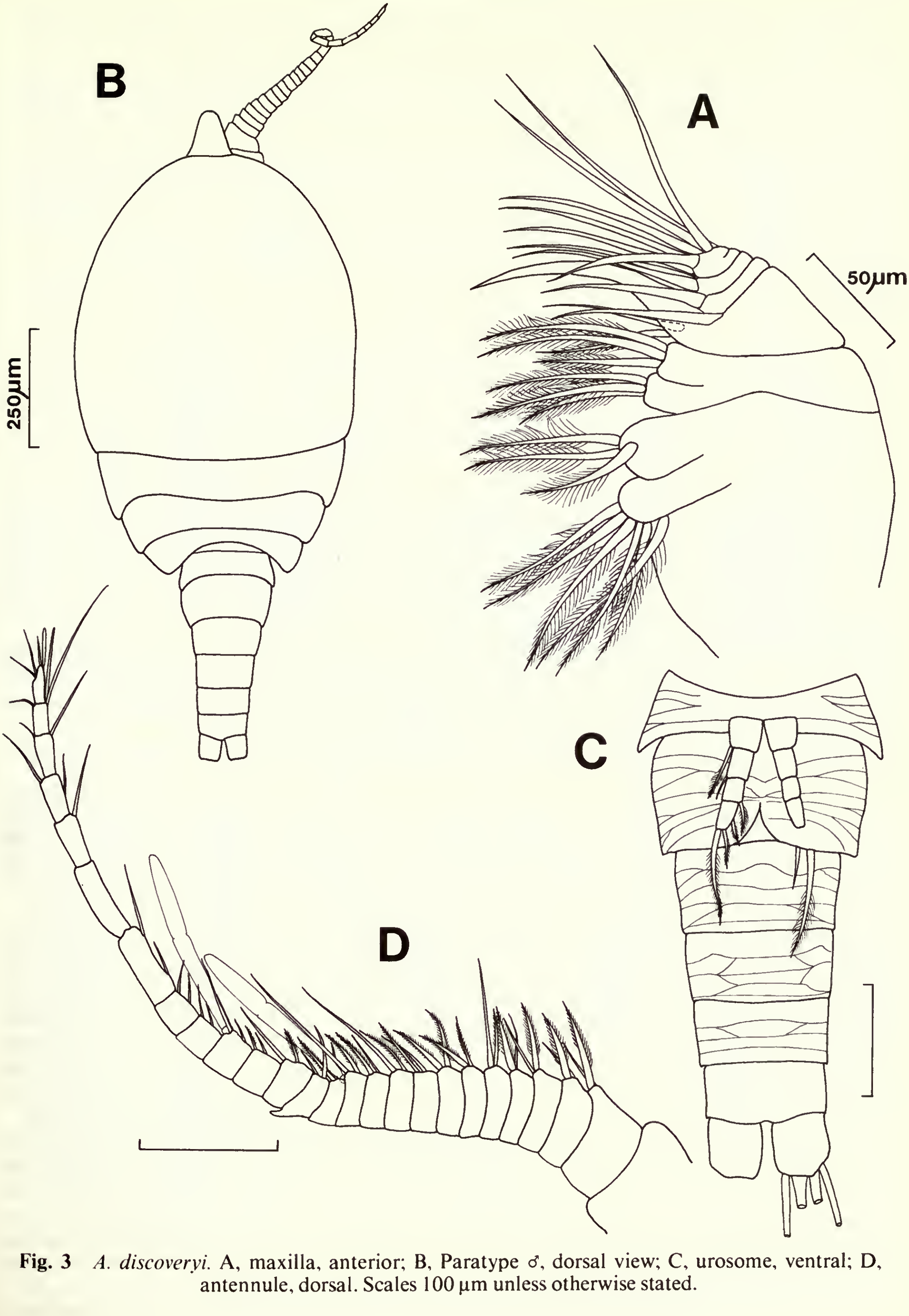

Fig. 3 *A. discoveryi.* A, maxilla, anterior; B, Paratype ♂, dorsal view; C, urosome, ventral; D, antennule, dorsal. Scales 100 µm unless otherwise stated.

Leg 6 (Fig. 1C) reduced to a semicircular flap closing off the opening of the genital antrum; bearing an outer plumose seta and a short inner spine.

Adult male (Fig. 3B) body length 1·1 to 1·3 mm (based on 3 specimens). Prosome and urosome (Fig. 3C) as in adult female. Appendages as in female except for antennules and legs 5 and 6.

Antennules (Fig. 3D) 25-segmented, unigeniculate with the articulation between segments XIX and XX. Armature elements as follows: I–2, II–2, III–2, IV–2, V–2, VI–2, VII–2, VIII–2, IX–2, X–2, XI–2+1 aesthetasc, XII–2, XIII–2, XIV–2, XV–4, XVI–2+1 aesthetasc, XVII–2, XVIII–2, XIX–2, XX–0(?), XXI–1, XXII–2, XXIII–2, XXIV–2+1 aesthetasc, XXV–3+1 aesthetasc. Segment XIII with a spinous process at posterolateral angle.

Legs 1–4 (Figs 4A-D) biramous with 3-segmented rami; armature formula as follows:

	coxa	basis	endopod	exopod
leg 1	0–1	I–1	0–1;0–1;1,2,3,	I–1;I–1;III,I,3
leg 2	0–1	I–0	0–1;0–2;1,2,3	I–1;I–1;III,I,4
leg 3	0–1	1–0	0–1;0–2;1,2,3	I–1;I–1;III,I,4
leg 4	0–1	1–0	0–1;0–2;missing	I–1;I–1;III,I,4

Pinnule rows present on inner and outer margins of endopod segments and inner margins of exopod segments; spinules present along margins of exopod segments. All outer margin exopodal spines armed with bilateral strips of fine membrane, apical spine with membrane externally and pinnules internally. All setae plumose except for distalmost 2 inner margin setae on exopod of leg 4. These setae with blunt tips and rows of short stout pinnules, possibly representing a male dimorphic character.

Leg 5 (Fig. 4E) uniramous, 4-segmented and with bases of legs almost touching at ventral midline as in ♀. Segment 1 bearing 1 plumose seta at outer distal angle; segment 2 with naked seta in same position; segment 3 with plumose seta at inner distal angle; segment 4 with short inner margin plumose seta and 2 unequal plumose setae on distal margin.

Leg 6 (Fig. 3C) represented by a flattened plate bearing a long outer plumose seta and a short inner spine.

MATERIAL EXAMINED. Holotype ♀, 3 paratype ♂♂, 1 ♀, 2 Copepodid IV and 3 Copepodid III stages all from *Discovery* Stn 10379#37 (34°57′ N 32°55′ W) in the North Atlantic to the southwest of the Azores. Collected in RMT1+8M net system fished 23 to 56 m off the bottom in a water depth of about 3000 m. BM(NH) Registration Nos Holotype ♀ 1982.128, paratype ♀ 1982.129, ♂♂ 1982.130–132, Co. IV 1982.133–134 and Co. III 1982. 135–137.

REMARKS. The new genus differs from all known misophrioids, including those described herein, in the possession of an anteriorly directed rostrum. In other genera the rostrum is either ventrally directed (*Misophria* and *Misophriopsis* gen. nov.) or posteroventrally directed and fused to the labrum (*Benthomisophria* and *Misophriella* gen. nov.). Another remarkable feature of this genus is the large number of segments in the antennules of both sexes. The twenty-seven segments found in the female is the largest number recorded for any copepod, including the calanoids in which 25 is the largest number known. The phylogenetic significance of the multi-segmented antennules is discussed below.

The developmental stages of *A. discoveryi* will not be described as only the third (Co. III) and fourth (Co. IV) copepodid stages have been found. As in other misophrioids (Boxshall & Roe, 1980) the copepodid stages can be determined by the number of urosome somites, the Co. III having 3 and the Co. IV having 4. It is interesting to note that the segmentation of the antennule is complete (27 segments) at the Co. IV stage whereas in *Benthomisophria palliata* the complete complement of 18 segments is not achieved until the last moult into the adult. The third copepodid of *A. discoveryi* has a 24-segmented antennule.

The presence of a 3-segmented leg 5 in female and 4-segmented leg 5 in male *A. discoveryi*

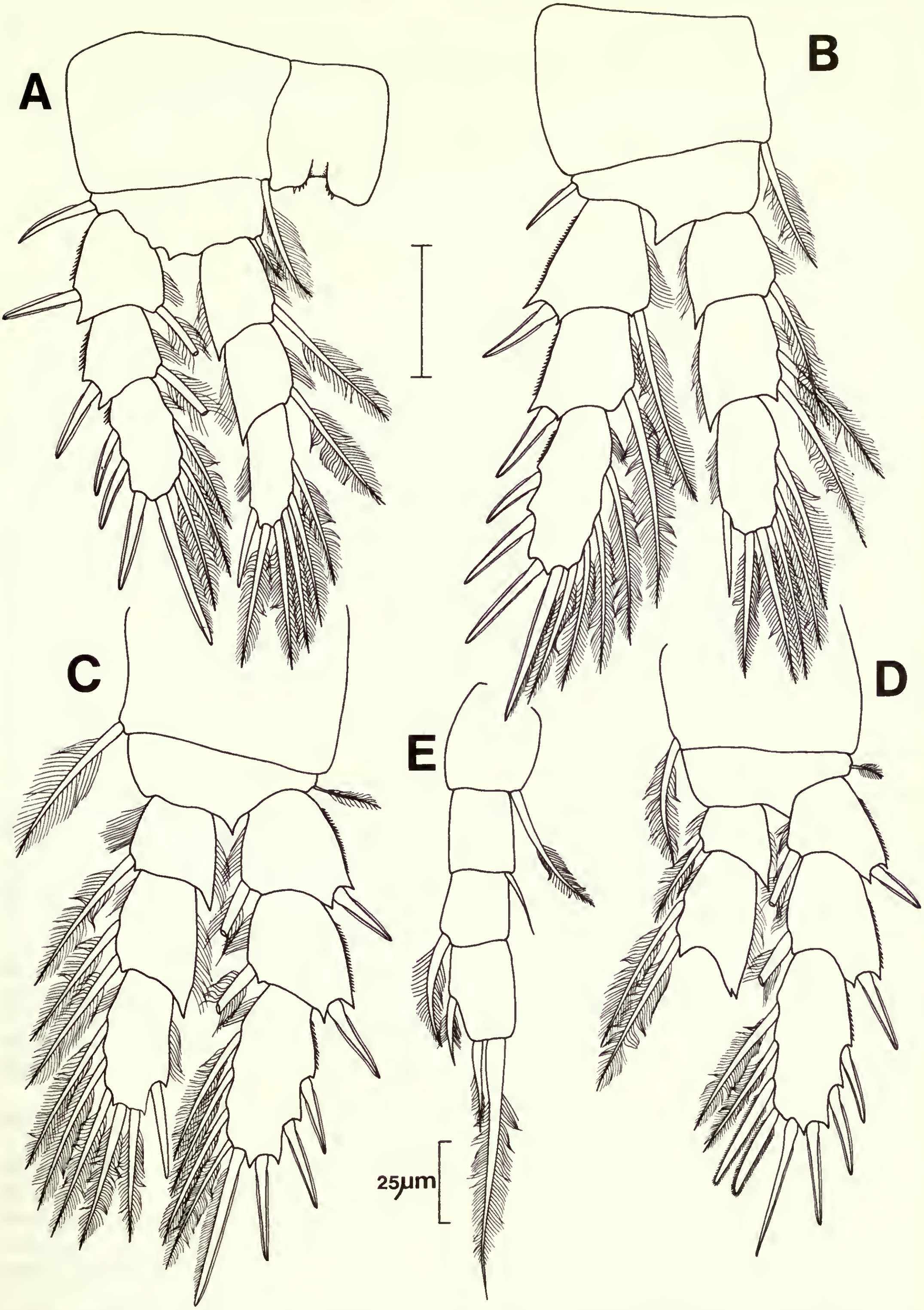

Fig. 4 *A. discoveryi.* A, leg 1, anterior; B, leg 2, anterior; C, leg 3, anterior; D, leg 4, anterior; E, leg 5, anteroventral. Scales 100 µm unless otherwise stated.

is the first documented example of sexual dimorphism in the fifth leg in misophrioids. In *Misophria* and *Benthomisophria* sexual dimorphism is restricted to the antennules and sixth legs. The presence of modified setae on the inner margin of the third exopod segment of leg 4 in male *A. discoveryi* may also represent sexual dimorphism but this cannot be confirmed until more material is obtained, as the only 2 females in the present material had incomplete fourth legs.

Genus *MISOPHRIELLA* nov.

DIAGNOSIS. As for type species.

TYPE SPECIES. *Misophriella tetraspina* gen. et sp. nov.

Misophriella tetraspina gen. et sp. nov.

Adult female (Fig. 5A) body length 0·87 mm (Holotype ♀). Prosome apparently 4-segmented but, as in all misophrioids, with the first free thoracic somite entirely concealed beneath a carapace-like extension of the posterior margin of the maxilliped-bearing somite. Nauplius eye absent. Rostrum posteroventrally directed and fused to anterior surface of labrum, not visible from dorsal aspect. Cone organs present in lateral areas on cephalosome. Urosome 6-segmented (Figs 6A-B), somites 2 to 5 each with a hyaline frill around posterior border. Anal somite with paired lobes dorsally, either side of anus and row of minute spinules around posterior margin. Pairs of pores present on both dorsal and ventral surfaces of anal somite. Caudal rami about as long as wide, armed with 2 long distal margin setae, 2 medium length distal angle setae, a dorsal seta near the distal margin, a seta near the middle of the lateral margin and a proximal setule on this margin.

Antennule (Fig. 5B) 19-segmented, articulating basally with a raised area of ventral cephalic surface. Armature elements as follows: I–1, II–9, III–2, IV–2, V–6, VI–2, VII–2, VIII–2, IX–2 + 1 aesthetasc, X–2, XI–2 + 1 aesthetasc, XII–2, XIII–2, XIV–2 + 1 aesthetasc, XV–1, XVI–1, XVII–2, XVIII–2 + 1 aesthetasc, XIX–6 + 1 aesthetasc. Segment I with 1 and segment II with 3 strong curved setae, each strongly sclerotized with an expanded base and a row of spinules along its convex margin.

Labrum large, posteriorly directed and fused with rostrum.

Antenna (Fig. 5C); basis with inner distal seta; 3-segmented endopod and 6-segmented exopod. Endopod segment 1 with a short plumose seta at inner distal angle; segment 2 with 2 short naked setae near middle of inner margin and a long and a short seta at inner distal angle; segment 3 with 6 long unilaterally plumose setae along its distal margin. Exopod segment 1 unarmed; segments 2 to 5 each with a single long, unilaterally plumose seta on its inner margin; segment 6 with 2 similar setae and a short plumose seta on its distal margin.

Mandible (Fig. 7A) with well developed gnathobase bearing 4 multicusped blades and some pinnules distally. Mandibular palp comprising basis, 2-segmented endopod and 4-segmented exopod. Basis apparently lacking inner distal angle seta. Endopod segment 1 with 1 naked seta at inner distal angle; segment 2 with 1 short naked seta and 4 long plumose setae apically. Exopod segment 1 unarmed; segments 2, 3 and 4 with 1, 2 and 3 long plumose setae respectively.

Maxillule (Fig. 7B) with armature of gnathobase reduced, comprising only 7 curved spinous elements, 1 hirsute seta and 2 slender naked setae. Endites 1 and 2 with 5 and 4 slender setae respectively; all setae sparsely armed with short spinules bilaterally. Outer lobe apparently absent. Maxillulary palp biramous with 1-segmented exopod and 3-segmented endopod. Endopod segment 1 fused to basis, with 3 unequal plumose setae at inner distal angle; segment 2 with 2 inner margin plumose setae; segment 3 small, bearing 4 unequal setae apically. Exopod with 3 long plumose setae distally and a short plumose seta and a row of pinnules along inner margin.

Maxilla (Fig. 7C) 6-segmented; segment 1 with 2 hemispherical endites, proximal endite with 1 naked and 4 plumose setae, distal endite with 2 spinulate setae; segment 2 with a

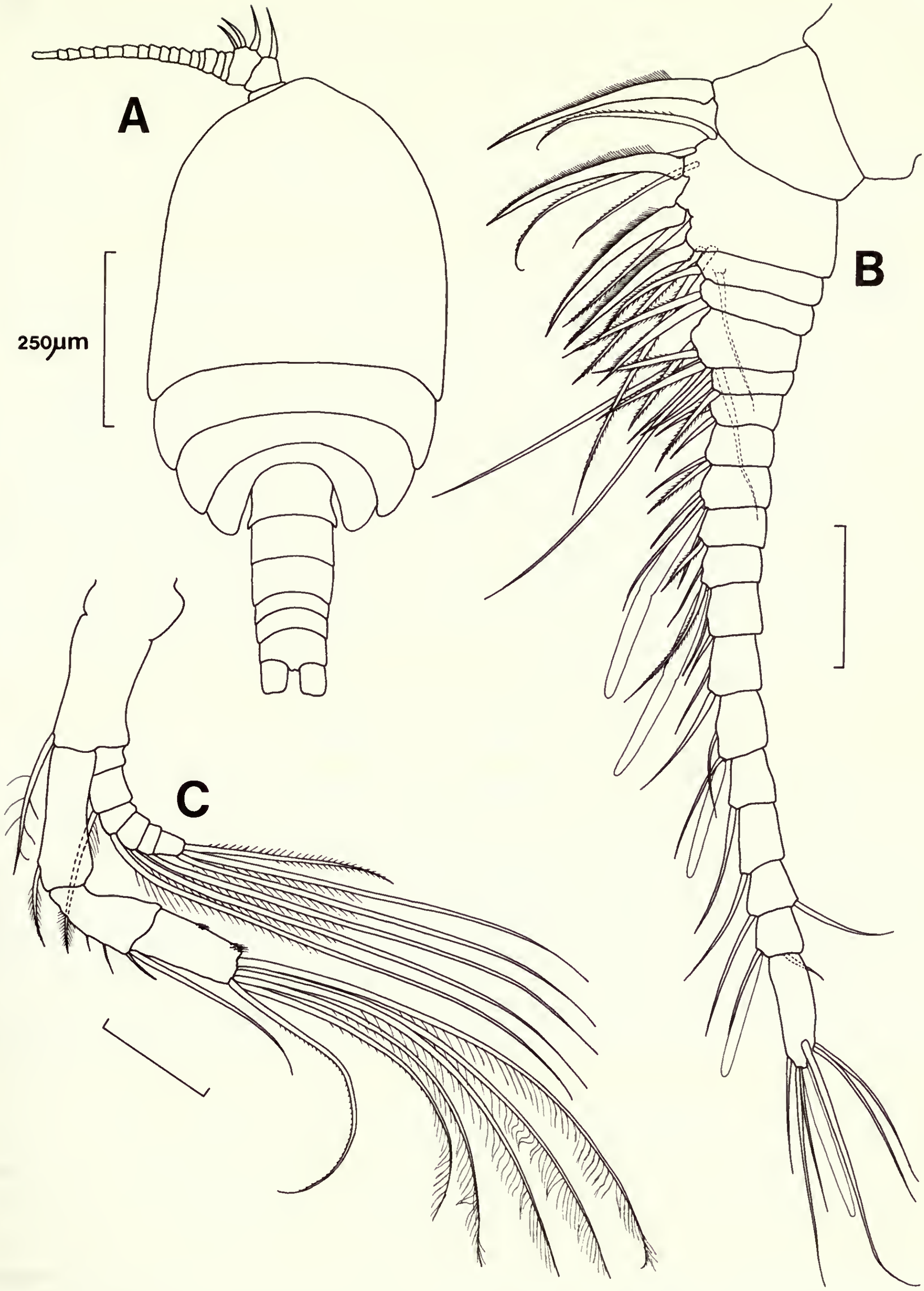

Fig. 5 *Misophriella tetraspina* gen. et sp. nov. Holotype ♀. A, dorsal view; B, antennule, dorsal; C, antenna, anterior. Scales 50 µm unless otherwise stated.

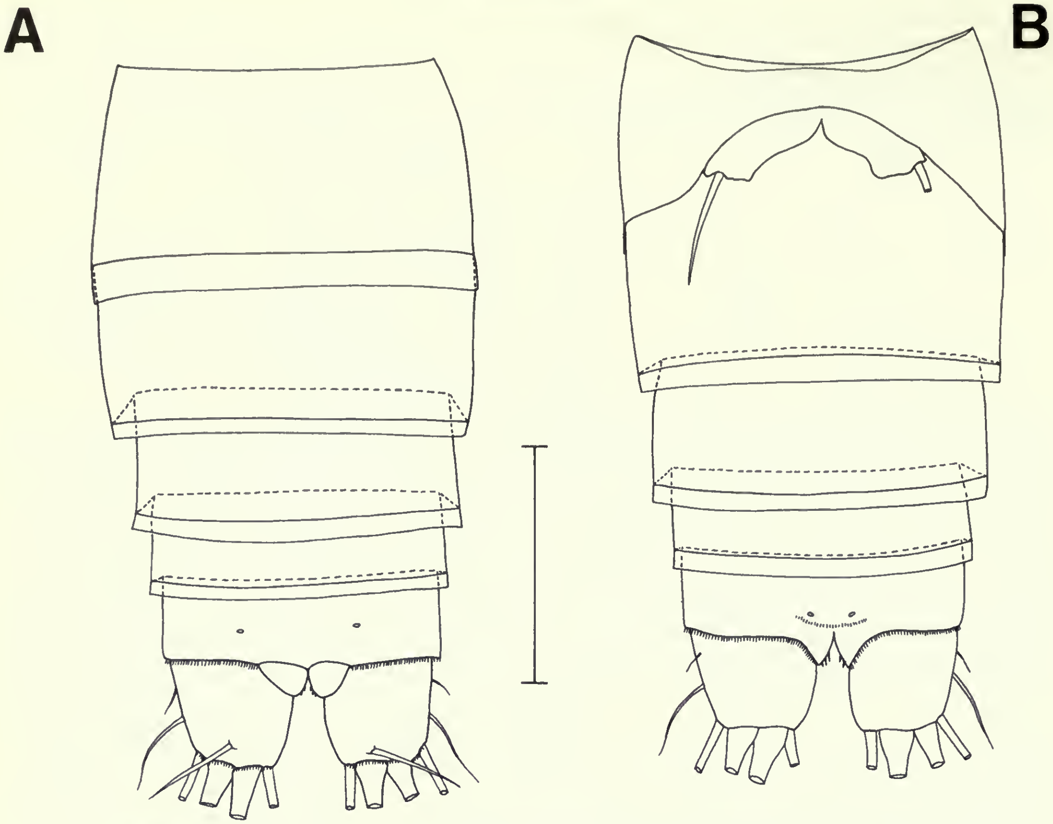

Fig. 6 *M. tetraspina.* A, urosome, dorsal; B, urosome, ventral. Scale 100 µm.

single elongate endite bearing 3 unequal naked setae at its apex; segment 3 produced into a long medial claw with a fringe of minute pinnules along its concave margin and 3 setae near its base; segments 4 to 6 each with 1 long, robust claw-like seta armed with a fringe of pinnules, segment 6 also bearing 2 slender apical setae.

Maxilliped (Fig. 7D) 7-segmented; segments 1 and 2 long and robust. Segment 1 armed with 1 proximal seta, 3 midmargin setae and 2 distal setae all on inner margin; segment 2 with 3 slender setae at middle of inner margin; segments 3 to 5 with 1, 2 and 1 slender inner margin setae respectively; segment 6 with an articulated seta distally and segment 7 with 2 similar articulated setae, plus 2 short naked setae.

Legs 1–4 (Figs 8 A-D) biramous, presumably with 3-segmented rami; armature formula as follows:

	coxa	basis	endopod	exopod
leg 1	0–1	I–1	0–1;0–2;1,2,3	I–1;I–1;III,I,4
leg 2	0–1	1–0	0–1;missing	I–1;I–1;missing
leg 3	0–1	1–0	0–1;0–2;missing	I–1;missing
leg 4	0–1	1–0	0–1;0–2;missing	I–1;missing

Pinnule rows present on inner and outer margins of endopod segments and on inner margins of exopod segments. Leg 1 with accessory digitiform processes on outer margin of exopod segments 2 and 3 between bases of spines. Exopod spines armed with bilateral strips of serrate membrane.

Leg 5 (Fig. 8E) uniramous, 4-segmented. Segment 1 broader than long, unarmed; segment

2 broader than both segments 1 and 3, armed with a naked seta on outer margin; segment 3 with spinous process at outer distal angle; segment 4 with 1 plumose seta either side of central spine in distal margin, also with an inner margin plumose seta on left leg but not on right.

Leg 6 (Fig. 6B) forming a curved plate on ventral surface of genital somite; armature incomplete.

MATERIAL EXAMINED. Holotype ♀ collected at *Discovery* Stn 10379#37 (34°57′ N 32°55′W) in the North Atlantic southwest of the Azores. Caught in RMT1+8M net system fished 23 to 56 m off the bottom in a water depth of about 3000 m. BM(NH) Registration No. 1982·138.

REMARKS. The new genus differs from all known misophrioids, including those described herein, in the form of the maxillule (which has a 3-segmented endopod, no outer lobe and an elongate exopod bearing only 4 setae), in the presence of only a single endite on the second segment of the maxilla and in the number of segments in the antennule. This genus exhibits a general reduction in the numbers of armature elements on most of the mouthparts, particularly on the maxillulary palp and the maxilla. In addition to these quantitative differences there are also qualitative differences, such as the spiniform nature of 4 setae on the proximal segments of the antennule and the presence of articulated setae on the maxilliped.

The armature elements of the fifth legs provide some indication of the homology of the segments. The second segment carries an outer seta at its distal angle and it is also much wider than the other segments. It probably represents the basis. Segment 1 therefore represents the coxa, and segments 3 and 4 the 2-segmented exopod. The holotype exhibits bilateral asymmetry in the armature of leg 5 but it is assumed that this is an aberrant condition and is not indicative of a true asymmetry as displayed by the fifth legs of many calanoids.

Genus ***MISOPHRIOPSIS*** nov.

DIAGNOSIS. As for type species.

TYPE SPECIES. *Misophriopsis dichotoma* gen. et sp. nov.

Misophriopsis dichotoma gen. et. sp. nov.

Adult female (Fig. 9A) body length 0·9 mm (Holotype ♀). Prosome apparently 4-segmented but with first free thoracic somite entirely concealed beneath a carapace-like extension from the posterior margin of the maxilliped-bearing somite. Nauplius eye absent. Rostrum small, ventrally directed with its apex adjacent to, but not fused to, the labrum (Fig. 12). Cone organs present in lateral areas on either side of cephalosome. Urosome (Fig. 9B) 6-segmented. Caudal rami wider than long, armed with 2 long distal margin setae, a medium length seta at both inner and outer distal angles, another on the dorsal surface near bases of distal setae, and a short lateral seta.

Antennule (Fig. 9C) 18-segmented. Armature elements as follows: I–1, II–11, III–2, IV–6, V–2, VI–2, VII–2, VIII–2+1 aesthetasc, IX–2, X–2+1 aesthetasc, XI–2, XII–2, XIII–2+1 aesthetasc, XIV–1, XV–1, XVI–2, XVII–2+1 aesthetasc, XVIII–6+1 aesthetasc. Spinules present on posterior surface of segment II.

Labrum (Fig. 12) large, posteriorly directed but not fused with rostrum; armed with 2 large medially directed spinous processes on its posterior margin.

Antenna (Fig. 9D) basis lacking inner distal seta; endopod 3-segmented, exopod 6-segmented. Endopod segment 1 with 2 inner distal setae; segment 2 with 3 setae spaced along inner margin; segment 3 with 5 long distal margin setae. Exopod segment 1 unarmed; segment 2 with 2 inner margin setae; segments 3 to 5 each with a single seta at inner distal angle; segment 6 with 3 plumose setae.

Mandible (Fig. 9E) with well developed gnathobase bearing distally 4 multicusped blades,

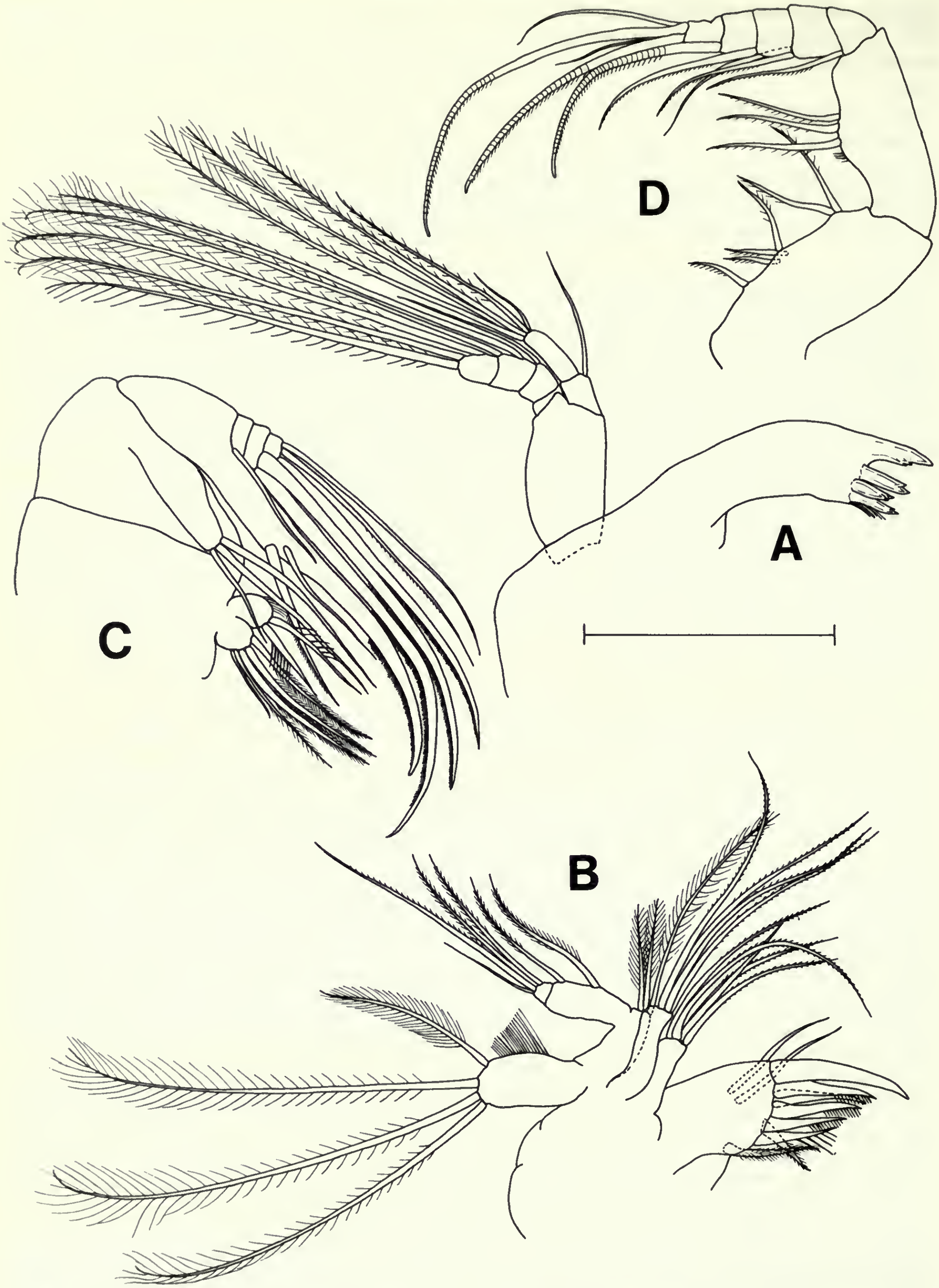

Fig. 7 *M. tetraspina.* A, mandible, anterior; B, maxillule posterior; C, maxilla, anterior; D, maxilliped, posterior. Scale 100 µm.

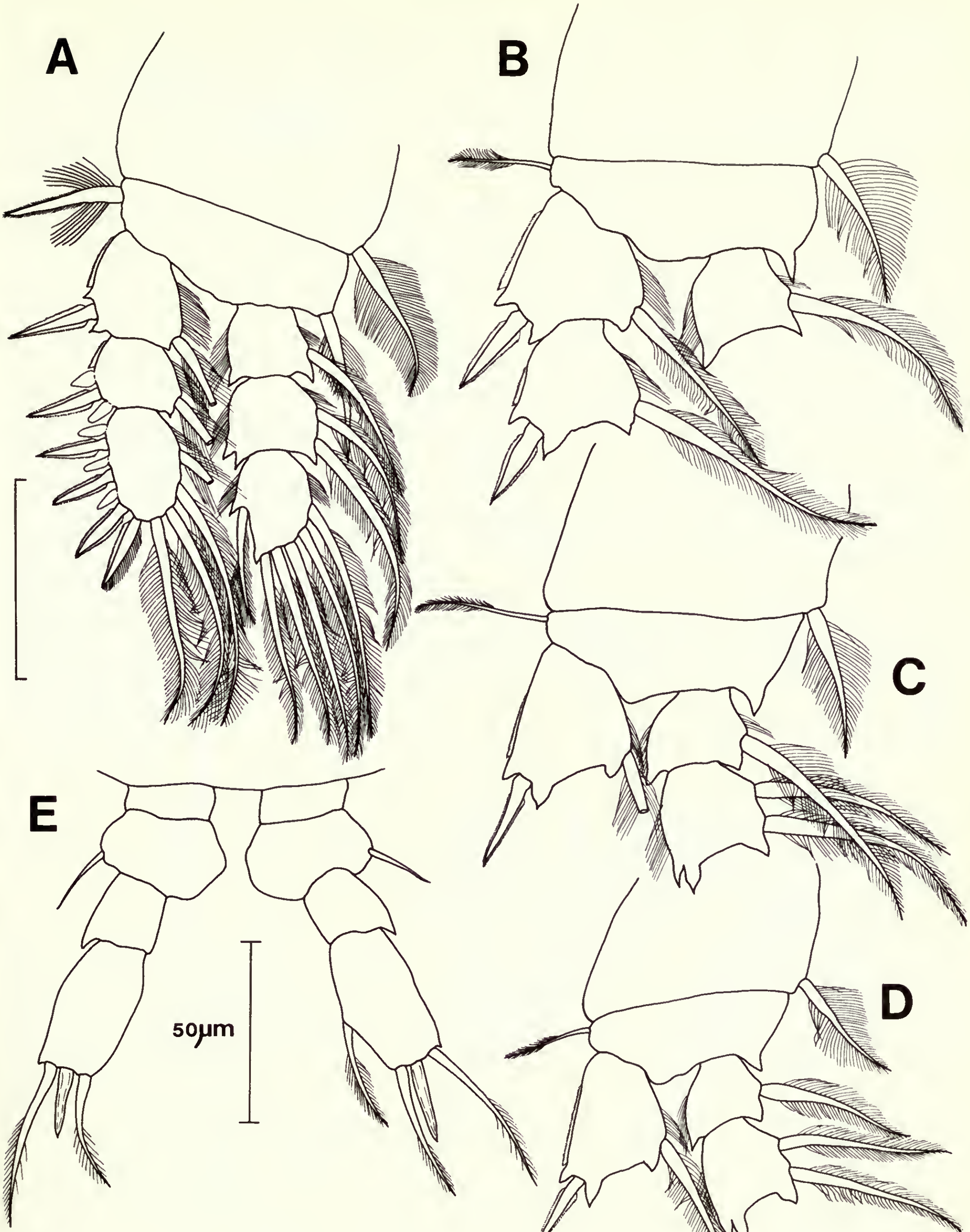

Fig. 8 *M. tetraspina.* A, leg 1, anterior; B, leg 2, anterior; C, leg 3, anterior; D, leg 4, anterior; E, leg 5, anteroventral. Scales 100 µm unless otherwise stated.

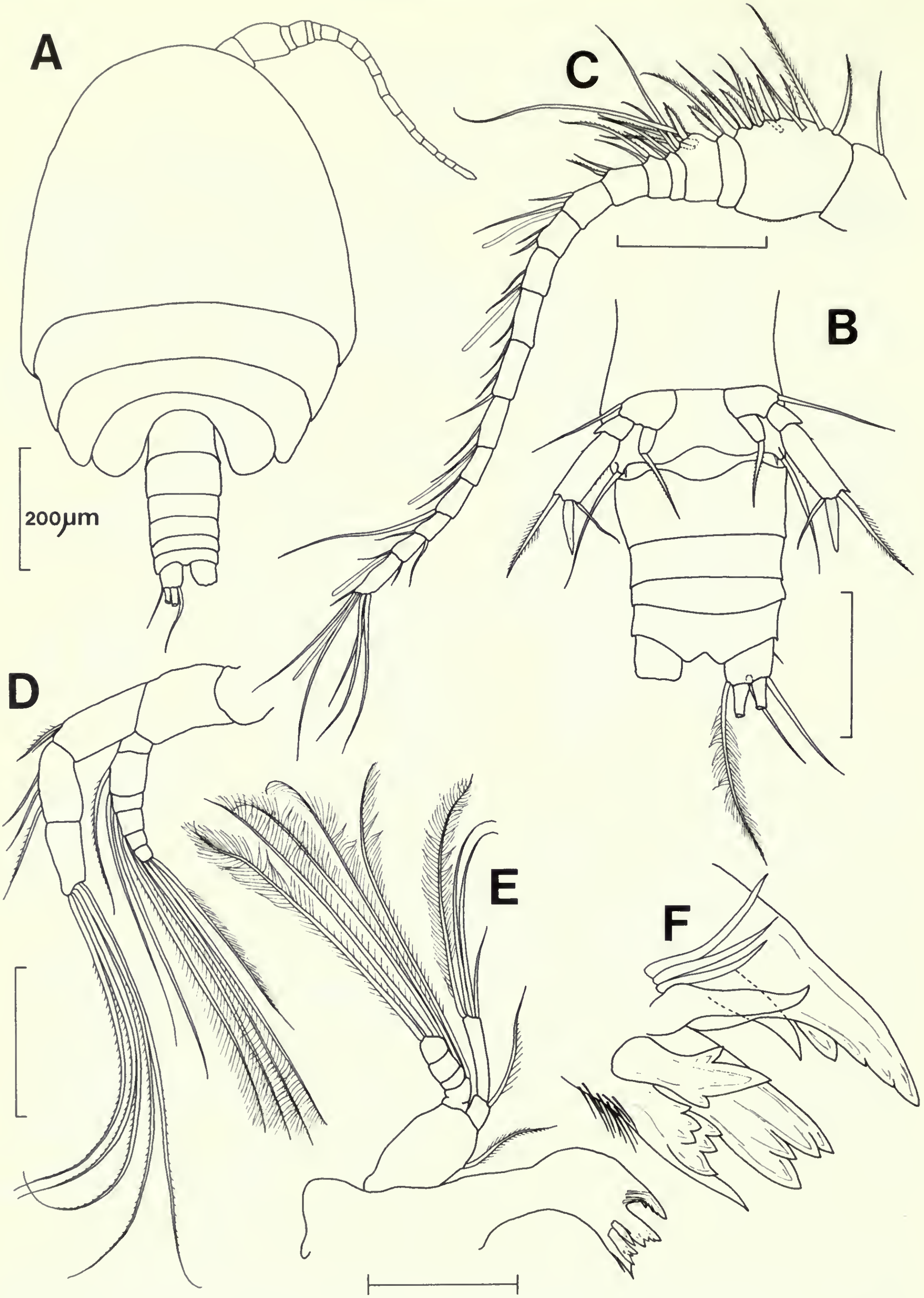

Fig. 9 *Misophriopsis dichotoma* gen. et sp. nov. Holotype ♀. A, dorsal view; B, urosome, ventral; C, antennule, dorsal; D, antenna, anterior; E, mandible, posterior; F, detail of mandibular gnathobase. Scales 100 μm unless otherwise stated.

several strong spines and a small subapical patch of pinnules. Mandibular palp comprising basis, 2-segmented endopod and an indistinctly 5-segmented exopod. Basis armed with a plumose seta midway along inner margin. Endopod segment 1 with plumose seta at inner distal angle; segment 2 elongate with 4 unequal setae on distal margin. Exopod segments 1 and 2 incompletely separated; segment 1 unarmed; segments 2 and 3 each with a plumose seta at inner distal angle; segment 4 probably with inner seta, missing from dissected appendage but its presence indicated by a scar on the surface of the segment; segment 5 with 1 inner and 2 distal margin setae.

Maxillule (Fig. 10A), gnathobase with 7 distal margin spines, 2 hirsute setae and 3 naked setae subapically on the posterior surface, and 2 plumose setae on a spinulate swelling on the anterior surface. Endite 1 short and slightly furrowed on its posterior surface, armed with 6 apical plumose setae. Endite 2 long, with 3 apical plumose setae. Outer lobe rudimentary, represented by 8 plumose setae on outer surface of segment. Maxillulary palp biramous with 2-segmented endopod and 1-segmented exopod; segment 1 of endopod fused to basis, with junction marked by 2 subapical setae. Endopod segment 1 with 4 plumose setae at inner distal angle; segment 2 with 3 naked setae arising proximal to the midpoint of the inner margin, 3 similar setae arising subapically on same margin, and 5 setae on distal margin. Exopod with 9 plumose inner and distal margin setae of varying lengths and with fringes of long pinnules proximally.

Maxilla (Fig. 10B) 6-segmented; segment 1 with 5 plumose setae on proximal endite and 3 on distal endite; segment 2 with 3 plumose setae on both proximal and distal endites; segment 3 produced medially into a curved claw armed with 2 naked setae near its base; segments 4 to 6 with a total of 7 naked setae.

Maxilliped (Fig. 10C) 7-segmented, although proximal segment showing some signs of subdivision at midlength. Segment 1 bearing 4 plumose setae and a short naked seta along inner margin, and some long pinnules proximally on outer margin; segment 2 with 3 inner margin plumose setae; segments 3 to 6 each with 2 long, unilaterally plumose setae at inner distal angle; segment 7 with 3 distal setae.

Legs 1–4 (Figs 11 A–D) biramous, with 3-segmented rami. Armature formula as follows:

	coxa	basis	endopod	exopod
leg 1	0–1	I–I	0–1;0–2;1,2,3	I–1;I–1;III,I,4
leg 2	0–1	1–0	0–1;0–2;1,2,3	I–1;I–1;III,I,5
leg 3	0–1	1–0	0–1;0–2;missing	I–1;I–1;III,I,5
leg 4	0–1	1–0	0–1;0–2;missing	I–1;I–1;III,I,5

Outer margins of all exopod segments with strips of serrated membrane. Rows of pinnules present on inner margins of all exopod segments and inner and outer margins of endopod segments. Outer margin spines of leg 1 armed bilaterally with fine strips of smooth membrane. Apical spines with short pinnules along inner margins, and strip of smooth membrane on outer margin in leg 1. Outer margin element on basis spinous on leg 1, setiform on legs 2 to 4.

Leg 5 (Fig. 11E) *biramous,* comprising unsegmented protopod, 2-segmented exopod and 1-segmented endopod. Basal seta present at outer distal angle of protopod. Exopod segment 1 unarmed, segment 2 with 3 distal margin elements, a long plumose outer seta, a median spine and an inner naked seta. Endopod with single plumose seta apically.

Leg 6 (Fig. 11F) with transverse intercoxal sclerite joining members of leg pair reduced to a slender bar. Leg comprising an outer process with a long apical seta, a median spine and an inner spinous process.

MATERIAL EXAMINED. Holotype ♀ collected at *Discovery* Stn 10379 #37 (34°57′ N 32°55′ W) in the North Atlantic to the southwest of the Azores. Caught in RMT1+8M net system fished 23 to 56 m off the bottom in a water depth of about 3000 m. BM(NH) Registration No. 1982·139.

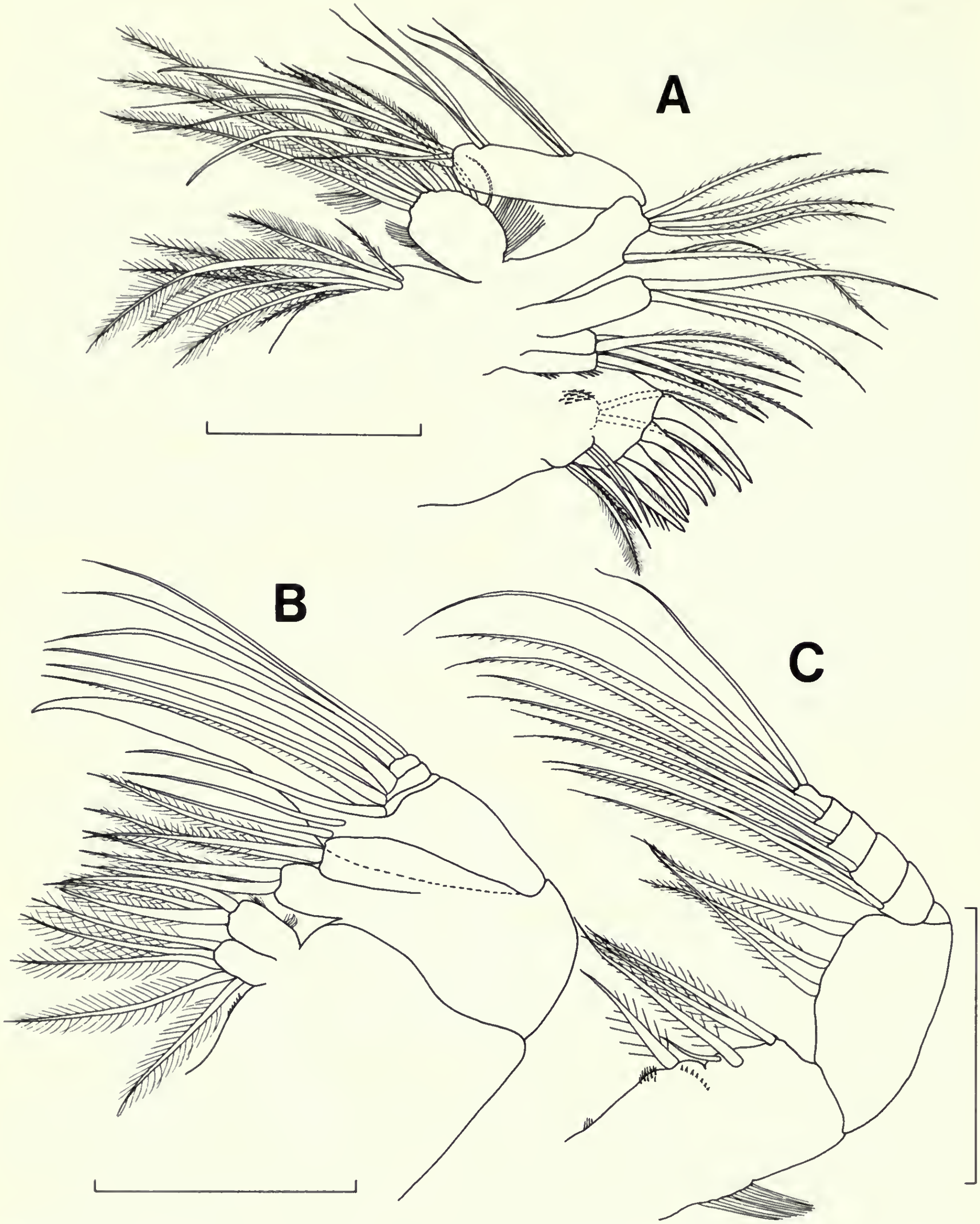

Fig. 10 *M. dichotoma.* A, maxillule, posterior; B, maxilla, anterior; C, maxilliped, anterior. Scales 100 µm.

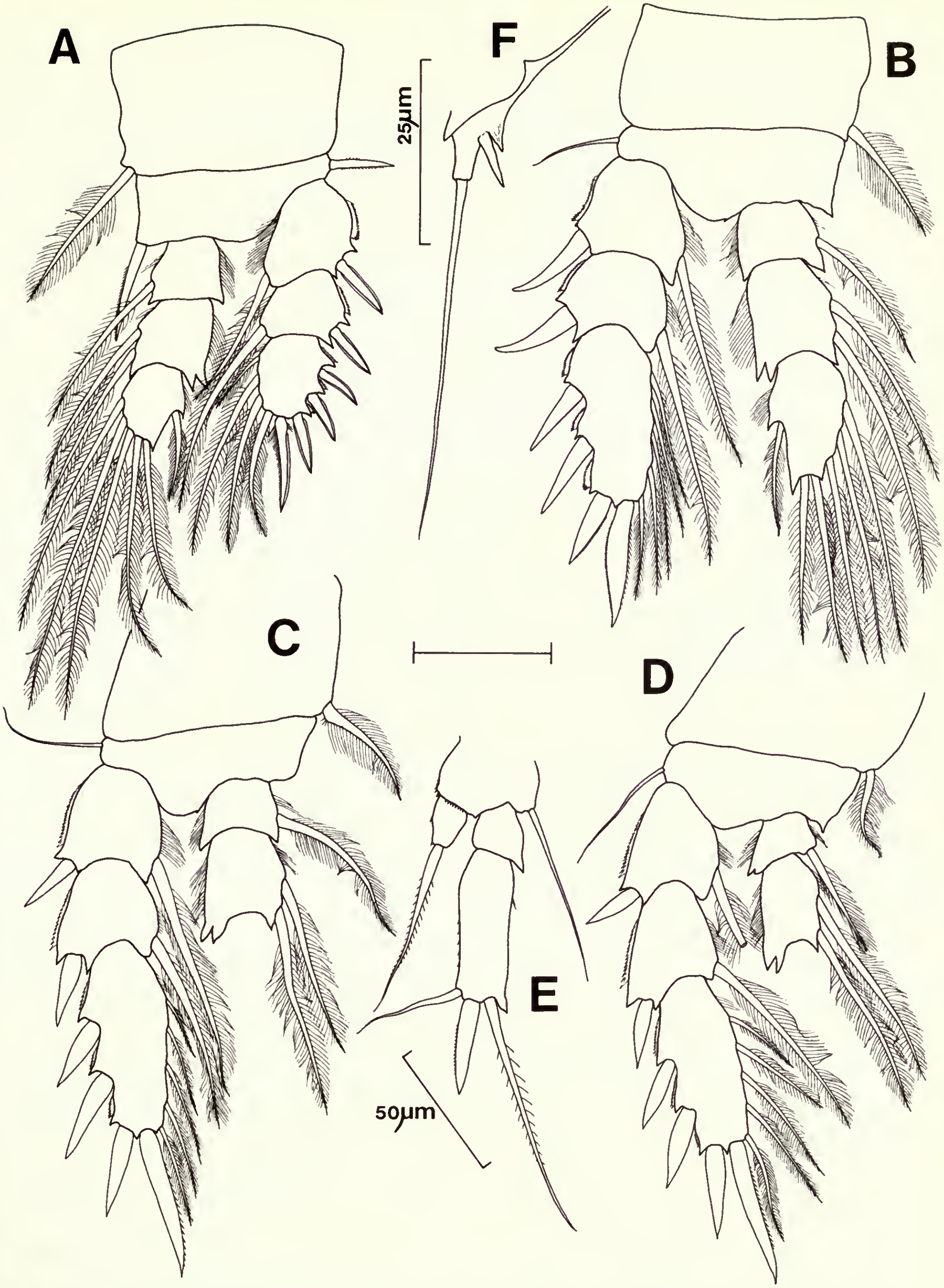

Fig. 11 *M. dichotoma.* A, leg 1, anterior; B, leg 2, anterior; C, leg 3, anterior; D, leg 4, anterior; E, leg 5, anteroventral; F, leg 6, ventral. Scales 100 µm unless otherwise stated.

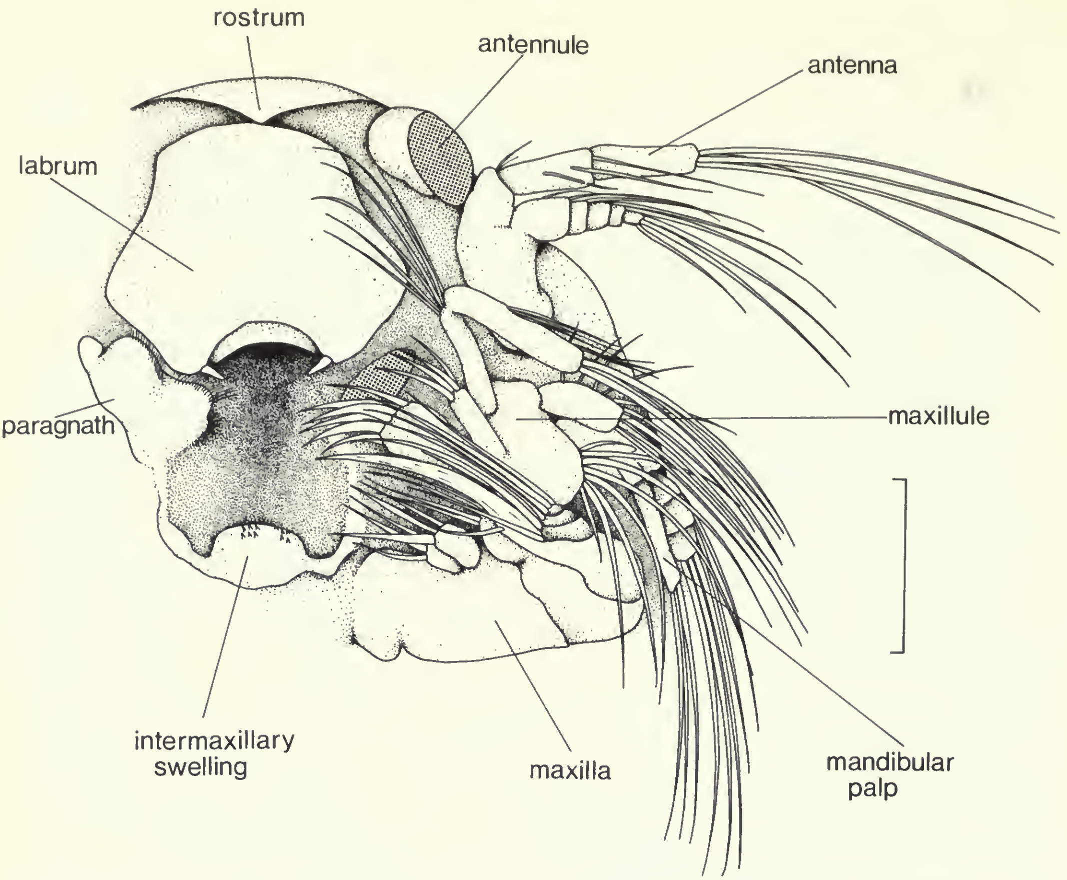

Fig. 12 *M. dichotoma*. Ventral view of mouthparts of left side, with antennule, left paragnath and mandibular gnathobase removed. Scale 100 μm.

Remarks. The new genus differs from all known misophrioids, and from all known podopleans, in the possession of a biramous fifth leg. It also differs from other misophrioid genera in the presence of a pair of large spinous processes on the posterior margin of the labrum. The arrangement of the mouthparts (Fig. 12) is very similar to that of *Benthomisophria palliata*. The antennae and mandibular palps are both reflexed so that their setae will sweep over the areas of cone organs located laterally on the cephalosome as in *Benthomisophria*.

Key to genera and species of the Misophrioida

1. Large anteriorly directed rostrum visible in dorsal view; antennule with 25 (♂) or 27 (♀) segments. . . . . ***Archimisophria discoveryi***
Rostrum ventrally or posteroventrally directed, not visible in dorsal view; antennule with less than 25 segments 2
2. Leg 5 biramous, with 1-segmented endopod and 2-segmented exopod . . . . ***Misophriopsis dichotoma***
Leg 5 uniramous, with 1 to 4 segments 3
3. Leg 5 4-segmented, antennule with 19 segments (♀) . . . . ***Misophriella tetraspina***
Leg 5 with less than 4 segments, antennule with less than 19 segments (♀) 4
4. Leg 5 3-segmented; antennule with 13 segments (♂) or 16 segments (♀) ***Misophria pallida***
Leg 5 2-segmented, comprising a triangular proximal segment and short distal segment; antennule with 18 (♀) or 16 (♂) segments . . . . ***Benthomisophria palliata***
Leg 5 1-segmented; antennule with 16 segments (♀ & ♂) . . . . . . ***B. cornuta***

Discussion

These three new genera exhibit between them an unusual array of plesiomorphic characters, many of which are present in a state approaching that attributed to the hypothetical ancestor of the Copepoda as a whole (see discussion in Boxshall *et al.*, in press). The antennae, for example, are biramous with an 8-segmented exopod and a 3-segmented endopod in *Archimisophria*, and the mandibles have a well developed gnathobase plus a biramous palp with a 5-segmented exopod and 2-segmented endopod in *Misophriopsis*. The basic structure of both these limbs is the same as that proposed for the ancestral copepod. The detailed structure of the maxillule was not considered in the discussion reported by Boxshall *et al.* (in press) but in my opinion the misophrioid pattern of large gnathobase, 2 other endites, 1 setose outer lobe, a 1-segmented exopod and a 3-segmented endopod, with the first segment fused to the basis, may well be similar to that possessed by the ancestral copepod. The misophrioid maxilla comprises 6 segments, the first 2 each bear a pair of setose endites, the third a claw-like endite, and the fourth to sixth variable number of inner and distal setae. This is close to what may be considered to be the ancestral copepod pattern. The 8-segmented maxilliped of *Archimisophria* consisting of a 3-segmented protopod and 5-segmented endopod is also very similar to the 9-segmented basic copepod maxilliped favoured by Gurney (1931) in his analysis of copepod appendages.

All these misophrioid features closely approximate to those exhibited by the plesiomorphic calanoids. It is the common possession of these calanoid-like gnathostomatous mouthparts and the possession of a heart that indicates that the Misophrioida diverged from the podoplean lineage soon after its separation from the gymnoplean lineage. The discovery of a 27-segmented antennule in *Archimisophria* and of a biramous fifth leg in *Misophriopsis* clearly demonstrates that the Misophrioida has diverged less from the common ancestral stock of the Copepoda than any other podoplean group.

The possession of a biramous fifth leg is of great phylogenetic significance. The difference between the normal biramous fifth swimming leg of gymnopleans and the reduced uniramous fifth leg of podopleans led Giesbrecht (1899) to suggest the possibility that they are not homologous. Gurney (1931) rejected this and suggested that the typical uniramous leg of podopleans represents the exopod of an originally biramous limb. This interpretation has been widely adopted and the presence, in *Misophriopsis*, of a biramous fifth leg in which the endopod is reduced to a single segment bearing a single seta provides further confirmation. The fifth leg undergoes considerable reduction within the Misophrioida. In *Misophria* the endopod is represented by a single median seta on the distal margin of the unsegmented protopod, although the exopod is similar to that found in *Archimisophria*. In *Benthomisophria cornuta* the fifth leg is reduced to a single segment.

The 27-segmented antennule of female *Archimisophria* is of interest because of the considerable controversy that exists (see Boxshall *et al.*, in press) concerning the nature of this limb in the ancestral copepod. Giesbrecht (1892 & 1899) analysed the segmentation and armature of the antennules of many calanoid and other copepods in an attempt to reduce the antennule of all copepods to a common type. Giesbrecht's basic copepod antennule was 25-segmented and by studying the arrangement of the armature elements he was able to determine which segments had fused in those forms with fewer segments. This basic limb closely resembles that of *Calanus finmarchicus* Gunnerus, 1770 both in number of segments and in setation. The typical armature present on each antennulary segment is 2 setae and 1 aesthetasc, at least in the female, although one or more of these elements is often lost, most commonly the aesthetasc. Even the arrangement of these 3 elements, which Giesbrecht called a 'trithek', follows a constant pattern. One seta, the proximal seta, is positioned about midway along the anterior margin of the segment whereas the other seta, the distal seta, and the aesthetasc are positioned close together at the distal angle of the anterior margin. The typical trithek may have been different for the male, because a proximal and a distal seta plus 2 distal aesthetascs are commonly found, as for example, in *Eucalanus attenuatus* Dana, 1849. Some of the more distal segments have modified tritheks. In female *Calanus*

Table 1. The structure and armature of copepod antennules. A comparison between a gymnoplean *(Calanus finmarchicus)*, a podoplean *(Archimisophria discoveryi)* and their hypothetical common ancestral form

Calanus finmarchicus ♀																												
armature	S	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	D	D	P	P	p	A
segmentation	1		2			3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Archimisophria discoveryi ♀																												
armature	S	t	t	t	T	t	t	T	t	t	t	T	t	t	t	t	T	t	t	t	t	t	d	d	p	p	P	A
segmentation	1		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Common ancestral pattern ♀																												
armature	S	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	D	D	P	P	P	A
segmentation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28

Where S=single seta, T=typical trithek, t=trithek without the distal aesthetasc, D=trithek without the proximal seta, d=trithek without the proximal seta and the aesthetasc, P=trithek with a posterior margin seta instead of the proximal seta, p=trithek with a posterior seta instead of the proximal seta but without the aesthetasc, A=apical elements.

finmarchicus segments 20 and 21 have no proximal seta, segments 22, 23 and 24 have no proximal seta but have instead a distal seta on the posterior margin, and the terminal segment 25 has an increased armature of up to 6 setae and an aesthetasc (see Table 1). As Gurney (1931) noted, many calanoids possess 3 complete tritheks on the second segment and a single proximal seta plus a distal trithek on the first segment. He interpreted this as evidence that the second segment of calanoid antennules is derived from 3 fused segments and that the first segment may be derived from 2 fused segments. On the basis of this interpretation he postulated that the ancestral copepod antennule comprised 27 or possibly 28 segments. The discovery of *Archimisophria* with its 27-segmented antennules provides a remarkable corroboration of Gurney's hypothesis.

Comparison between the antennules of female *Calanus finmarchicus* and *Archimisophria discoveryi* is made in Table 1. The precise correspondence in the position of typical tritheks, denoted by T or t, and of modified tritheks, denoted by D or d and P or p, in these two taxa is remarkable as they are drawn from the 2 main copepod lineages, Gymnoplea and Podoplea. It is possible from the comparison in Table 1 to identify a common pattern from which both may be derived by reduction. I suggest that this pattern may well represent that found in the common ancestor of the Copepoda.

Functional interpretation of the unique characters exhibited by misophrioids (Boxshall, 1982 & in press) suggests that the ancestral misophrioid stock became adapted to a bathypelagic existence and to gorging as a feeding strategy. The group appears to have radiated in the deep-sea near-bottom environment and it is probable that many new misophrioid taxa will be discovered as the near-bottom community is subject to more intense study. Despite their obvious specializations the misophrioids also retain many characters of the presumed ancestral copepod stock and it is clear that they diverged from the ancestral podoplean stock soon after it had attained its characteristic division into prosome and urosome.

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Larval development of British prawns and shrimps (Crustacea: Decapoda: Natantia) 4. *Palaemon (Palaemon) serratus* (Pennant, 1777) and functional morphology of swimming

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Introduction

Palaemonid shrimps are widely distributed in the N.E. Atlantic being found in fresh water, in estuaries, intertidally and down to 40 m offshore, but their larvae are rare in the plankton. All decapod larvae have a natural tendency to sink (Foxon, 1934) and in order to maintain position at a particular depth (Savage, 1926) and perform daily vertical migrations (Russell, 1925, 1927; Hardy & Bainbridge, 1954), active upward swimming is necessary also. Foxon measured rates of movement in various decapods including pandalid carideans and several authors have noted the effect of light and gravity on the orientation and movement of decapod larvae (Sollaud, 1921; Gurney, 1942; Forward & Cronin, 1978).

The aim of this paper is to review the larval development of *Palaemon (Palaemon) serratus* (Pennant, 1777) and report on morphological adaptations, and a mechanism using many-jointed plumose setae fringing the thoracic exopods, for larval swimming.

Materials and Methods

Rearing

Ovigerous *Palaemon (Palaemon) serratus* were trawled from 12 m in April 1979 from Plymouth Sound, Devon (Grid reference: SX 475512). Similar rearing techniques to those reported previously (Fincham 1977, 1978, 1979) were used with the following modifications:

1. The controlled temperature room was at 14 °C.
2. Antibiotics were used for the first three stages only (Fincham, 1979).

Larval material has been deposited in the Crustacea collection of the BM(NH), registration number 1982 : 186.

Telson morphology

The telson was removed from larvae by a cut at the narrow junction with the abdomen, rinsed in distilled water, freeze dried, mounted end-on with Araldite on stubs, coated with gold and examined with a scanning electron microscope.

Palaemon (Palaemon) serratus (Pennant, 1777)

Astacus serratus Pennant, 1777
Melicerta triliana Risso, 1816
Palaemon trilianus Risso, 1826
Palaemon treillianus H. Milne Edwards, 1837
Leander latreillianus Czerniavsky, 1884

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Table 1 Larval development and range of morphological and meristic variation in *Palaemon (Palaemon) serratus*
R = rudimentary; + = present/yes; – = absent/no; W = wide; N = narrow

	Zoea/Moult									
	1	2	3	4	5	6	7	8	9	PL1
Carapace										
No. of dorsal spines	0	1	2	3	3	3	3	3	3	7(3)[1]
No. of ventral rostral spines	0	0	0	0	0	0	0	0	0	2(0)[1]
Supraorbital spines +/–	–	+	+	+	+	+	+	+	+	–(+)[1]
No. of antero-lateral spines	0	1	1	2	2	2	2	2	2	2
Rostrum tip – downturned +/–	–	+	+	+	+	+/–	+/–	+/–	–	–
Ventral retrorse hooks +/–	+	–	–	–	–	–	–	–	–	–
	One group					two or more groups				
Antenna 1	1W,2N	2W,2N	3W	3W,1N	3W,1N	3W,1N 2 or 3N	4W 3N (1N)	2–3 groups	3–4 groups	4 or more
Stylocerite +/–	–	R	+	+	+	+	+	+	+	+
Statocyst +/–	–	–	–	–	R	R	R	R	+	+
No. of segments flagellum internal	0	0	1	1	1	1	1	1	1–2	5
external	1	1	1	1	1	1	1	1	2	7
Accessory flagellum +/–	–	–	–	–	–	–	–	–	–	R
Antenna 2										
Endopodite – No. of segments	1	1	3	3	3–4	4–5	5–7	6–7	9–12	many
Length of scapthocerite	0·64:1 to 0·71:1	0·65:1 to 0·74:1	0·69:1 to 0·75:1	0·75:1 to 0·81:1	0·80:1 to 0·88:1	<	=	=	>	>
Exopodite – No. of distal segments	5	4–5	3	0	0	0	0	0	0	0
No. of plumose setae	9+2	15+2 to 17+2	19+2 to 21+2	22+2 to 24+2	24–26	28–31	29–32	31–34	35–39	⩾40
Mandible – External spine +/–	–	–	–	–	–	–	–	–	–	+
Lacinia mobilis +/–	+	+	+	+	+	+	+	+	+	–
Palp	–	–	–	–	–	–	–	–	–	–
Maxilla 1										
No. of endite setae – Coxa	6	6	6	7	7	7–8	7–8	7–8	8–9	>9
Basis	5	7	7	8	8	8–9	8–9	8–9	9–13	⩾13

Maxilla 2										
No. of endite setae – Coxa	4	4	4	4	4	4	4	4	4	0
Basis 1	3	3	3	3	3	3–4	4	4	4–5	10
Basis 2	4	4	4	4	4	4	4–6	4–6	6	>12
Endopodite	3	3	3	3	3	3	3	3	3	2
No. of plumose setae exopodite	5	7–8	10–12	12–14	16–18	19–22	21–25	23–31	26–35	>40
Maxilliped 1										
No. of setae on internal margin – Coxa	1	1	1	1	1	1	1	1	1	8
Basis	6	6	6	7	7	9	9–10	11–13	14–20	>30
Exopodite – No. of setae – Lateral	0	0	0	0	0	1	2–5	5–6	5–9	⩾9
Maxilliped 2										
Endopodite – No. of segments	4	4	4	4	4	4	4	4	4	5
Exopodite +/−	+	+	+	+	+	+	+	+	+	+
Setae +/−	+	+	+	+	+	+	+	+	+	+
Maxilliped 3										
Endopodite – No. of segments	4	5	5	5	5	5	5	5	5	5
Exopodite +/−	+	+	+	+	+	+	+	+	+	+
Setae +/−	+	+	+	+	+	+	+	+	+	+
Pereiopods 1 & 2 +/−	R	+	+	+	+	+	+	+	+	+
Biramous +/−	+	+	+	+	+	+	+	+	+	R
Endopodite – Propodus fixed finger +/−	−	−	−	−	+	+	+	+	+	+
Pereiopod 3 +/−	−	R	R	+	+	+	+	+	+	+
Biramous +/−		+	+	+	+	+	+	+	+	+
Pereiopod 4 +/−	−	R	R	R	+	+	+	+	+	+
Biramous +/−		+	+	+	+^{2}	+^{3}	+^{3}	+	+	+
Pereiopod 5 +/−	−	R	R	+	+	+	+	+	+	+
Biramous +/−		−	−	−	−	−	−	−	−	−
Abdomen										
Somite 5 – lateral spines +/−	−	+	+	+	+	+	+	+	+	+
Somite 6 – 'Continuous' with telson +/−	+	+	−	−	−	−	−	−	−	−
Pleopods +/−	−	−	−	−	R	R	R	R	+	+
Fringing setae					−	−	−	+/−	+/−	+
Appendix interna 2–5 +/−					−	−	−	−	+	+
Telson										
Posterior margin concave (−) or convex (+)	+/−	+/−	−	−	−	−	+/−	+	+	+
Spine formula	7+7	7+7	[1]6+ 6[1]	[3]4+ 4[3]	[3]4+ 4[3]	[3]4+ 4[3]	[3]4+ 4[3]	4+4	4+4	4+4
Small spines +/−	+	+	+	+	+	+	+	+	−	−
No. prs. of lateral spines	0	0	0	0	0	0	0	3	3	3
Uropods +/−	−	−	+	+	+	+	+	+	+	+
Long plumose setae – Endopodite			0	9–12	13–16	18–21	18–23	19–27	24–33	>36
Expodite			11–12	18–19	21–24	26–29	27–31	28–32	31–36	>39

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[1]intermediate form; [2]rudimentary fringing setae; [3]reduced fringing setae or of normal length.

Leander serratus Sharp, 1893
Leander treillianus Adensamer, 1898
Leander serratus var. *treillianus* De Man, 1915
Palaemon (Palaemon) serratus Holthuis, 1950

SYNOPSIS OF LARVAL DATA FROM PUBLISHED WORK. Thompson, 1836 zoeae I, III & V, p. 221, Figs 1–5, laboratory reared and plankton. Couch, 1845 zoea I, p. 20, no Figs, laboratory reared. Mayer, 1877 zoea I, telson, p. 250, Fig. 49. Keeble and Gamble, 1904 zoea I, chromatophores, p. 316. Sollaud, 1912 zoeae I–IX, p. 664, no Figs, laboratory reared. Williamson, 1915 zoea II (not I), Figs 120–125, zoea I Figs 126–128, last zoea Figs 129–132, p. 396, plankton. Sollaud, 1923 zoeae I–IX & post larva I, p. 530, plates 16–18 (Figs 1–4 only), laboratory reared and plankton. Reeve, 1969 zoeae I–V (XI), p. 77, no Figs, laboratory reared. Sutton *et al.*, 1969 zoea I, counting larvae, p. 433, Fig. 1, laboratory reared. Fincham & Williamson, 1978 key to larval stages.

In the following short descriptions of the key characters of the larval stages, setal counts have been omitted usually, but they are recorded in Table 1.

Description of larval stages

Key characters are printed in *italic type* and are useful for separating stages in British species.

ZOEA 1 (Fig. 1) 3·3 mm (3·2–3·5 mm)

Head (Figs 1a, b): *eyes sessile.*
Carapace (Figs 1a, b): *without spines,* rostrum straight or downcurved at tip, tapering distally, ventral margin with minute retrorse teeth distally, *equal to, or greater than, length of peduncle of antenna 1 but not reaching to end of antenna 1* (excluding terminal aesthetascs and setae).
Antenna 1 (Fig. 1c): peduncle bearing single flagellar segment with three aesthetascs distally, usually two narrow and one wide, occasionally 1 narrow and 2 wide.
Antenna 2 (Fig. 1d): exopodite as a broad lamina divided into 5 short segments distally, with 9+2 plumose setae on inner and distal margins. Endopodite of one segment (0·67 length of exopodite), with terminal plumose seta and short spine.
Mandibles (Fig. 1e): asymmetrical.
Maxillipeds 1–3 (Figs 1h–j): with natatory exopodites.
Pereiopods 1, 2 (Figs 1k, l): *rudimentary, biramous.*
Pereiopods 3–5: absent.
Abdomen (Figs 1a, b): *somite 5 with posterior margin rounded,* not produced into spines, somite six continuous with telson. No trace of pleopods.
Telson (Fig. 1p): fans out distally, posterior margin bears 7+7 plumose spines, with minute spines between four innermost spines.

ZOEA 2 (Fig. 2) 3·7 mm (3·5–3·9 mm)
Head (Figs 2a, b): *eyes stalked.*
Carapace (Figs 2a, b): *one dorso-medial and a pair of supra-orbital spines* all bent forward with small retrorse teeth, *rostrum without teeth, downturned at end to form small hook.*
Antenna 1 (Fig. 2c): *two peduncle segments, stylocerite forming on proximal external margin of first segment; single flagellar segment with four terminal aesthetascs, two wide and two narrow.*
Antenna 2 (Fig. 2d): exopodite with 4 or 5 short segments distally.
Pereiopods 1, 2 (Figs 2k, l): *developed with natatory exopodite.*
Pereiopods 3, 4 (Figs 2m, n): *rudimentary, biramous.*
Pereiopod 5 (Fig. 2o): *rudimentary, uniramous.*
Abdomen (Figs 2a, b): *somite 5 with posterior margin produced into a pair of conspicuous spines, somite 6 continuous with telson.*
Telson (Fig. 2p): *developing uropods visible beneath exoskeleton* alongside telson proper; *in central group of small spines, one pair longer than others.*

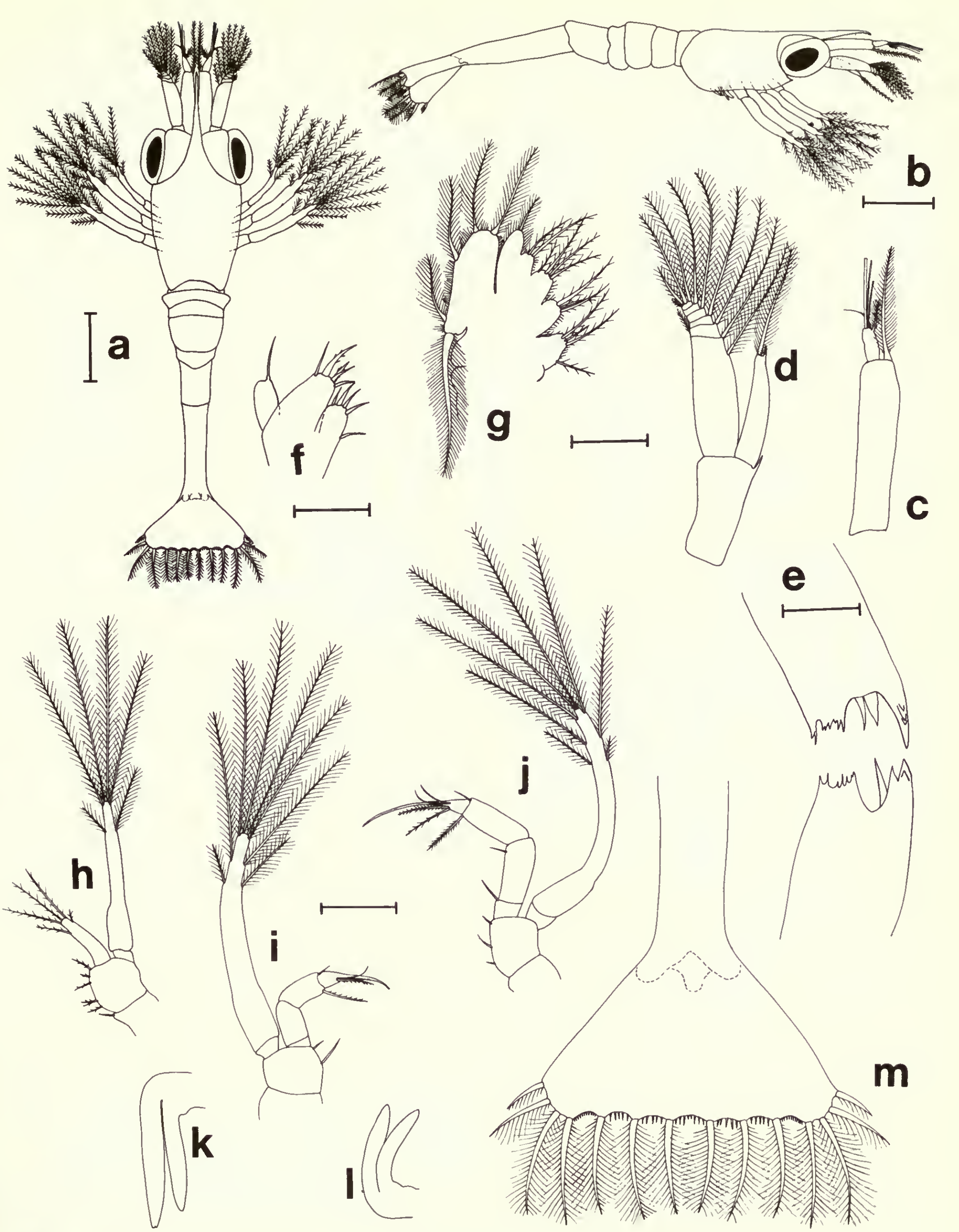

Fig. 1 Zoea 1: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) telson. Bar scales: a, b = 0·5 mm; c, d, h–m = 0·2 mm; g, f = 0·1 mm; e = 0·05 mm.

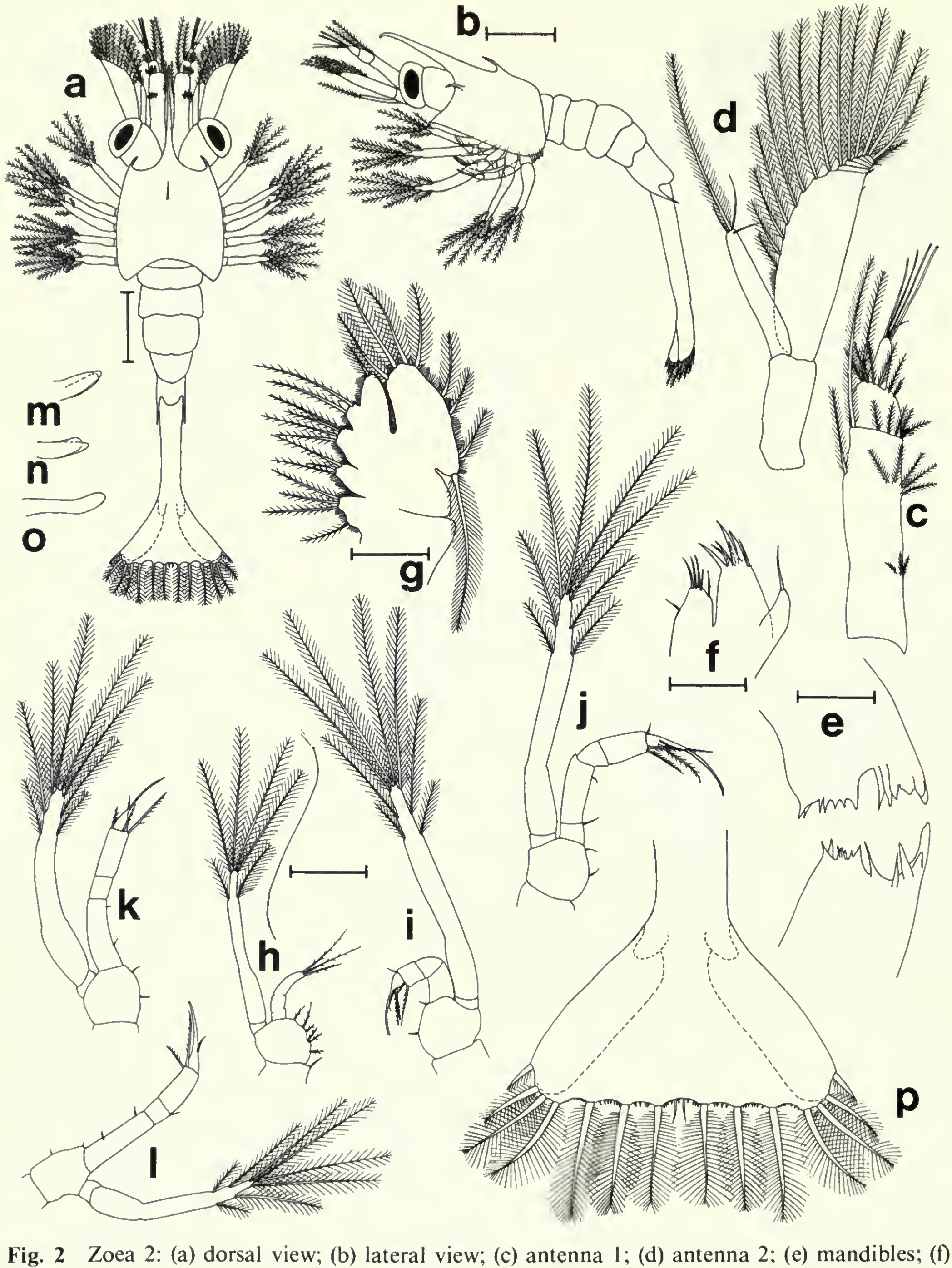

Fig. 2 Zoea 2: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson. Bar scales: a, b = 0·5 mm; c, d, h–p = 0·2 mm; g, f = 0·1 mm; e = 0·05 mm.

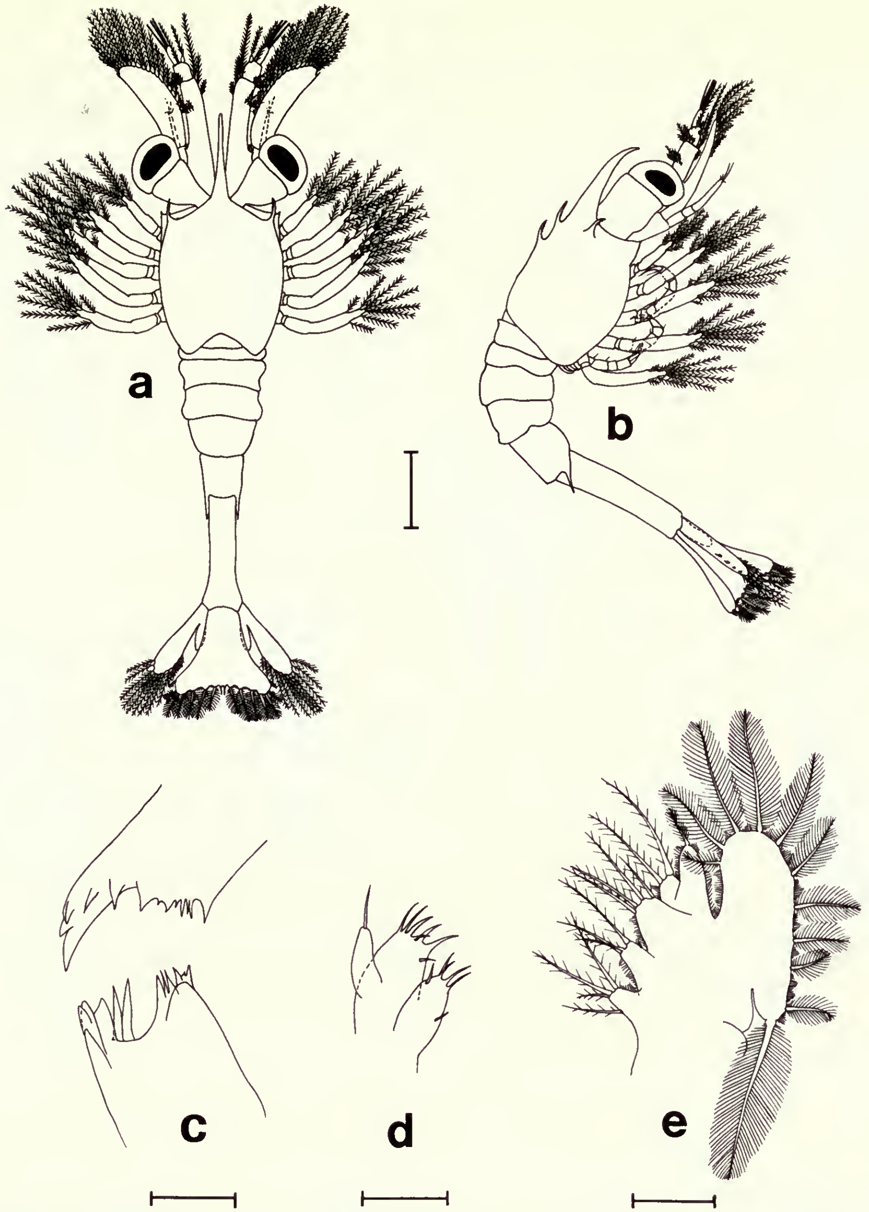

Fig. 3 Zoea 3: (a) dorsal view; (b) lateral view; (c) mandibles; (d) maxilla 1; (e) maxilla 2. Bar scales: a, b = 0·5 mm; c = 0·05 mm; d, e = 0·1 mm.

Zoea 3 (Figs 3, 4) 4·0 mm (3·7–4·3 mm)
Carapace (Fig. 3a, b): *two dorso-medial spines* and a small fronto-lateral spine at edge of carapace beneath the eyes, former with retrorse teeth ventrally.
Antenna 1 (Fig. 4a): *conspicuous spine medially,* stylocerite more pronounced; distal segment of peduncle bearing *first segment of internal flagellum,* single segment of *external flagellum bearing 3 wide aesthetascs distally.*
Antenna 2 (Fig. 4b, c): exopodite with distal part divided into 3 short segments; *endopodite of 3 segments.*

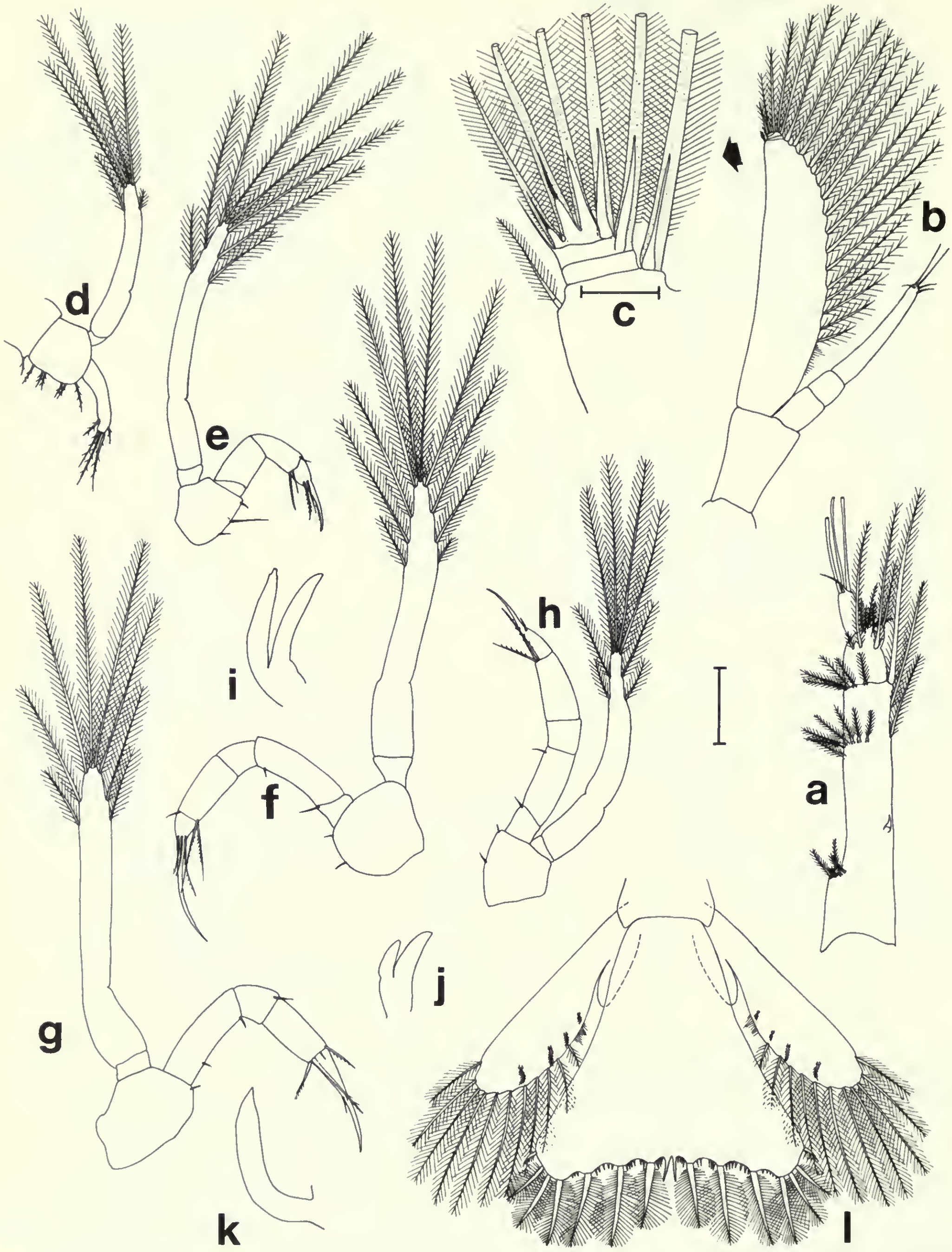

Fig. 4 Zoea 3: (a) antenna 1; (b) antenna 2; (c) distal part of exopodite of antenna 2; (d) maxilliped 1; (e) maxilliped 2; (f) maxilliped 3; (g) pereiopod 1; (h) pereiopod 2; (i) pereiopod 3; (j) pereiopod 4; (k) pereiopod 5; (l) telson. Bar scales: a, b, d–l = 0·2 mm; c = 0·05 mm.

Abdomen (Figs 3a, b, 41): *somite 6 divided from telson by suture. Uropod endopodite rudimentary with no marginal setae, exopodite with marginal setae.*
Telson (Fig. 41): narrower but still broader distally, outer pair of spines on posterior margin reduced.

Zoea 4 (Figs 5, 6) 4·5 mm (4·1–5·0 mm)
Carapace (Fig. 5a, b; Fig. 6a, b): *three dorso-medial spines* with retrorse teeth ventrally; pair of small fronto-lateral spines at edge of carapace beneath the eyes; *rostrum still downturned at end to form a small hook.*
Antenna 1 (Fig. 5c): *single segment of external flagellum bearing 3 wide and 1 narrow aesthetascs distally.*
Antenna 2 (Fig. 5d): distal part of exopodite no longer divided into segments.
Pereiopod 3 (Fig. 6h): *developed with natatory exopodite.*
Pereiopod 4 (Fig. 6i): *rudimentary, biramous.*
Pereiopod 5 (Fig. 6j): *developed, uniramous.*
Abdomen (Figs 5a, b): *endopodite and exopodite of uropod both with marginal plumose setae.*
Telson (Fig 6k): narrower but still broader distally; posterior margin weakly concave with *4+4 large spines,* the 3 outer spines on the latero-distal margin reduced (outer pair sometimes absent).

Zoea 5 (Figs 7–9) 5·5 mm (5·2–5·8 mm)
Carapace (Figs 7a, b): *rostrum still downturned to form a small hook.*
Antenna 1 (Fig. 8a): *rudiment of circular statocyst visible on first segment of peduncle.*
Antenna 2 (Fig. 8b): *endopodite of 3 or 4 segments.*
Pereiopods 1, 2 (Figs 9a, b): *endopodite with internal distal margin of propodus produced slightly forward* (will become fixed finger of chela).
Pereiopod 4 (Fig. 9d): *developed, exopod with rudimentary fringing setae.*
Telson (Fig. 9f): a little broader distally than proximally; spine formula as in Zoea 4 but with further reduction or even loss of small outer spines.
Abdomen (Fig. 7b): *somites 1–5 with rudimentary pleopods.*

Zoea 6 (Figs 10–12) 5·7 mm (5·2–7·4 mm)
Carapace (Figs 10a, b): rostrum weakly hooked at tip; *short plumose seta in angle of anterior dorso-medial spine.*
Antenna 1 (Fig. 11a): single external flagellum with four aesthetascs distally, *additional group of 2 or 3 narrow aesthetascs on internal margin.*
Antenna 2 (Fig. 11b): increase in number of segments of endopodite flagellum, *approximately equal to scaphocerite in length,* small spine on distal margin of peduncle segment.
Maxilla 2 (Fig. 11e): occasional increase in number of setae on basis 1.
Maxilliped 1 (Fig. 11f): *one plumose seta on proximo-lateral margin of exopod.*
Pereiopods 1, 2 (Figs 12a, b): *endopodite with internal distal margin of propodus produced foreward to almost half length of dactylus* (excluding terminal setae).
Pereiopod 4 (Fig 12d): exopodite occasionally with fringing plumose setae reduced.
Abdomen (Fig. 10b): pleopods on somites 1–5 rudimentary, biramous.

Zoea 7 (Figs 13–15) 6·1 mm (5·5–6·7 mm)
Carapace (Figs 13a, b): rostrum straight or weakly hooked at tip; *2 or 3 short plumose setae in angle of anterior dorso-medial spine.*
Antenna 1 (Fig. 14a): two or occasionally three groups of aesthetascs on internal margin of external flagellum.
Maxilla 2 (Fig. 14e): up to 6 setae on basis 2.
Maxilliped 1 (Fig. 14f): *2–5 plumose setae on proximo-lateral margin of exopodite.*
Pereiopods 1, 2 (Figs 15a, b): endopodite with internal distal margin produced forward to half length of dactylus (excluding terminal setae).

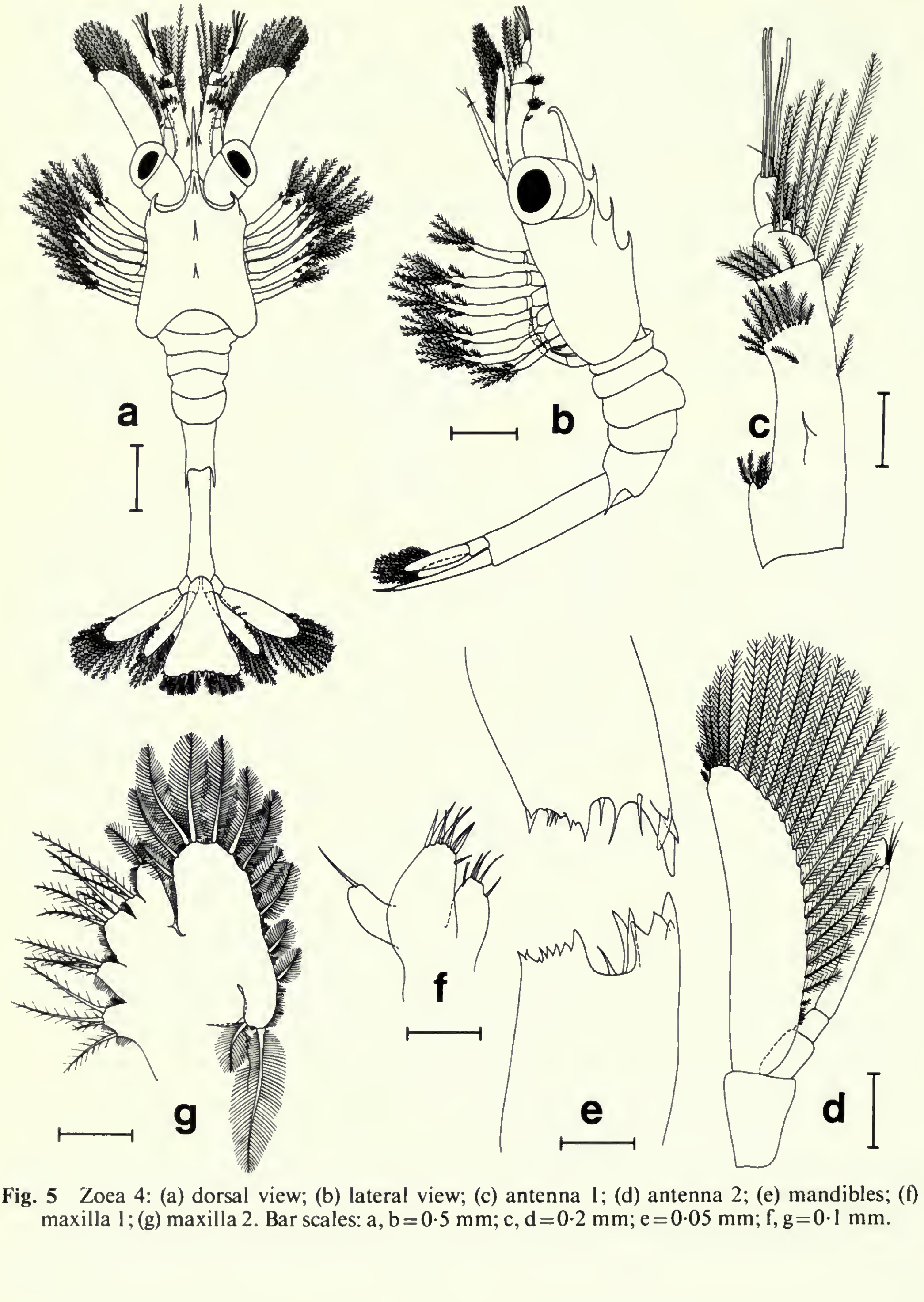

Fig. 5 Zoea 4: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2. Bar scales: a, b = 0·5 mm; c, d = 0·2 mm; e = 0·05 mm; f, g = 0·1 mm.

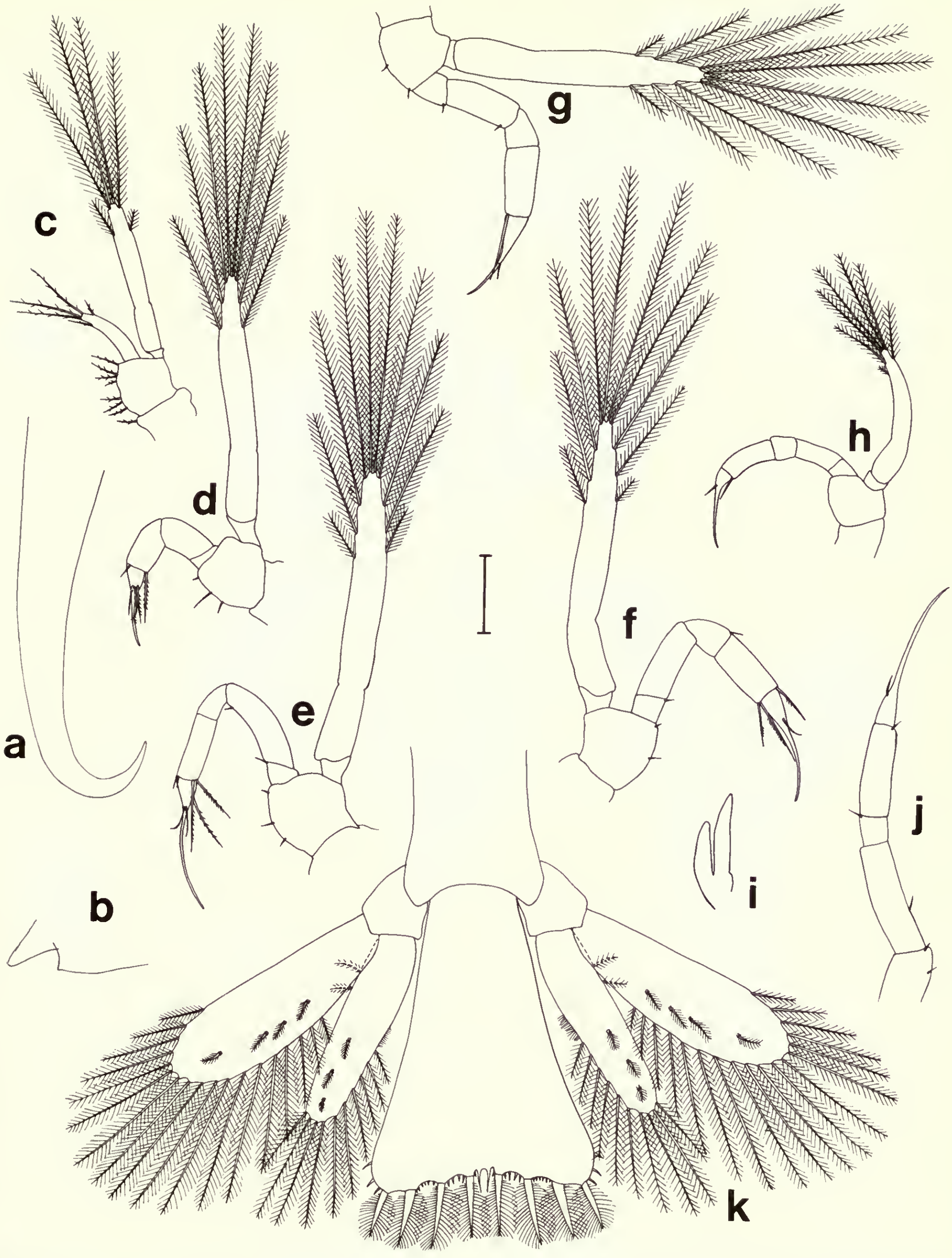

Fig. 6 Zoea 4: (a) tip of rostrum; (b) fronto-lateral corner of carapace; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5; (k) telson. Bar scales: a, b = 0·05 mm; c–k = 0·2 mm.

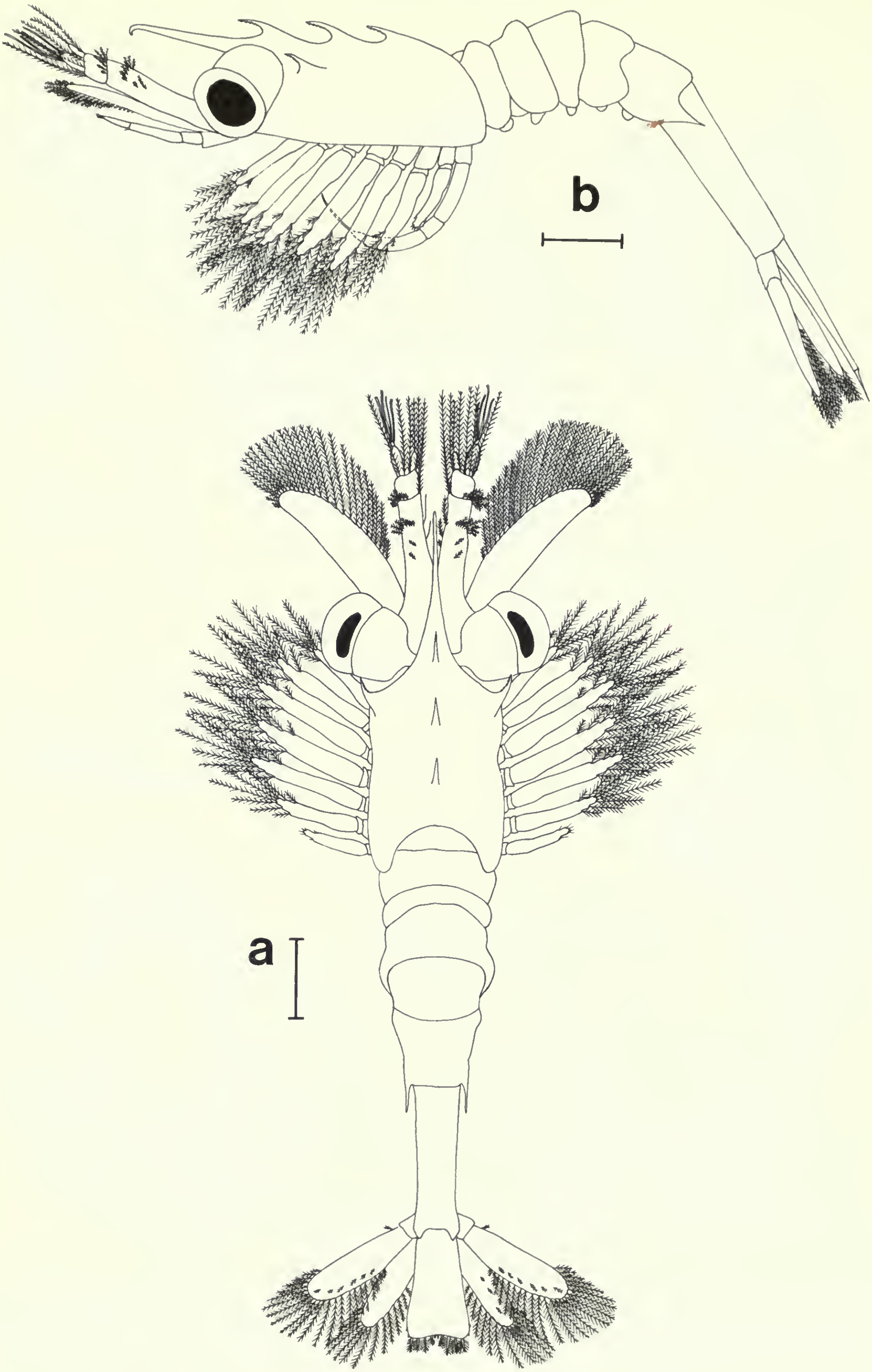

Fig. 7 Zoea 5: (a) dorsal view; (b) lateral view. Bar scales: 0·5 mm.

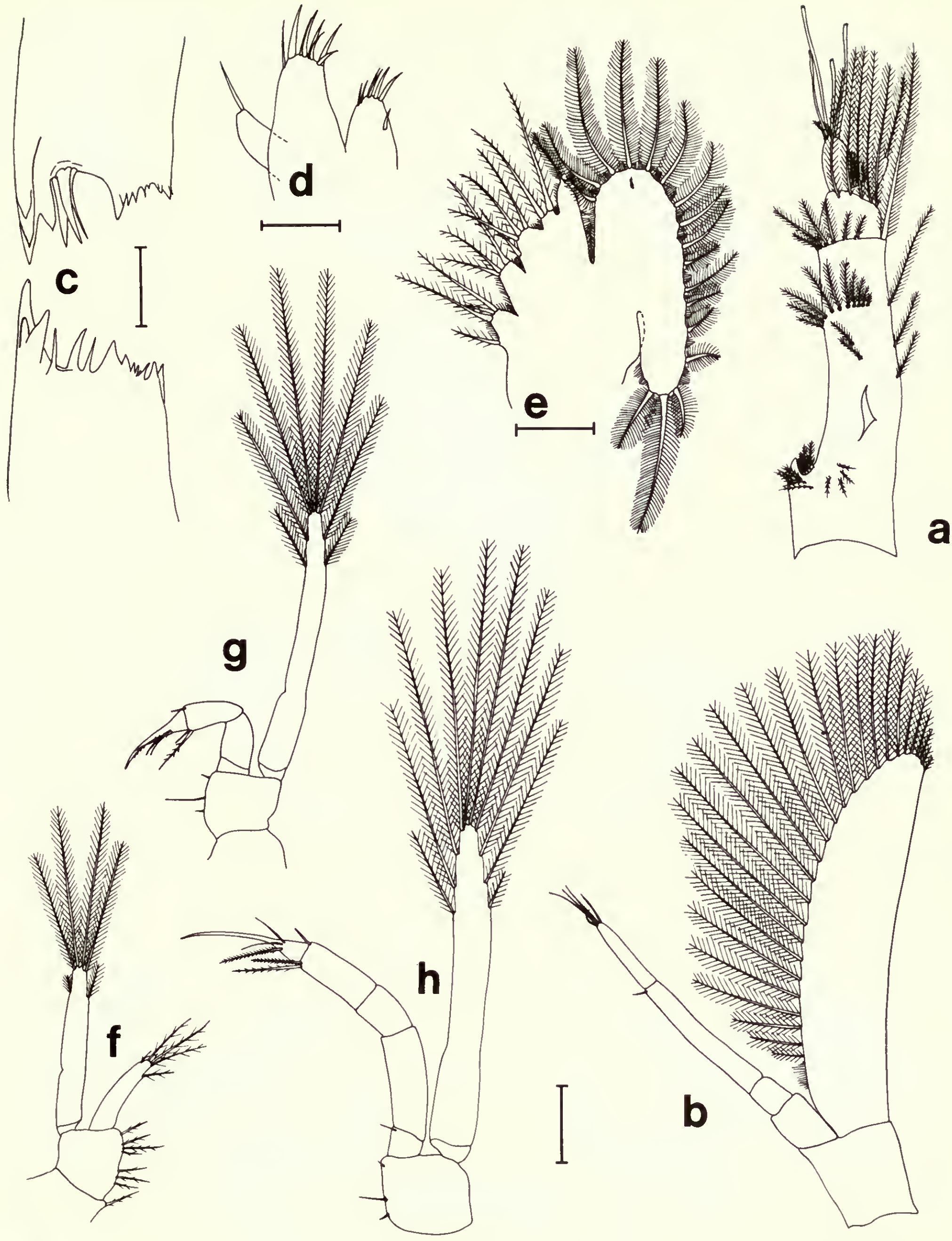

Fig. 8 Zoea 5: (a) antenna 1; (b) antenna 2; (c) mandibles; (d) maxilla 1; (e) maxilla 2; (f) maxilliped 1; (g) maxilliped 2; (h) maxilliped 3. Bar scales: a, b, f–h = 0·2 mm; c = 0·05 mm; d, e = 0·1 mm.

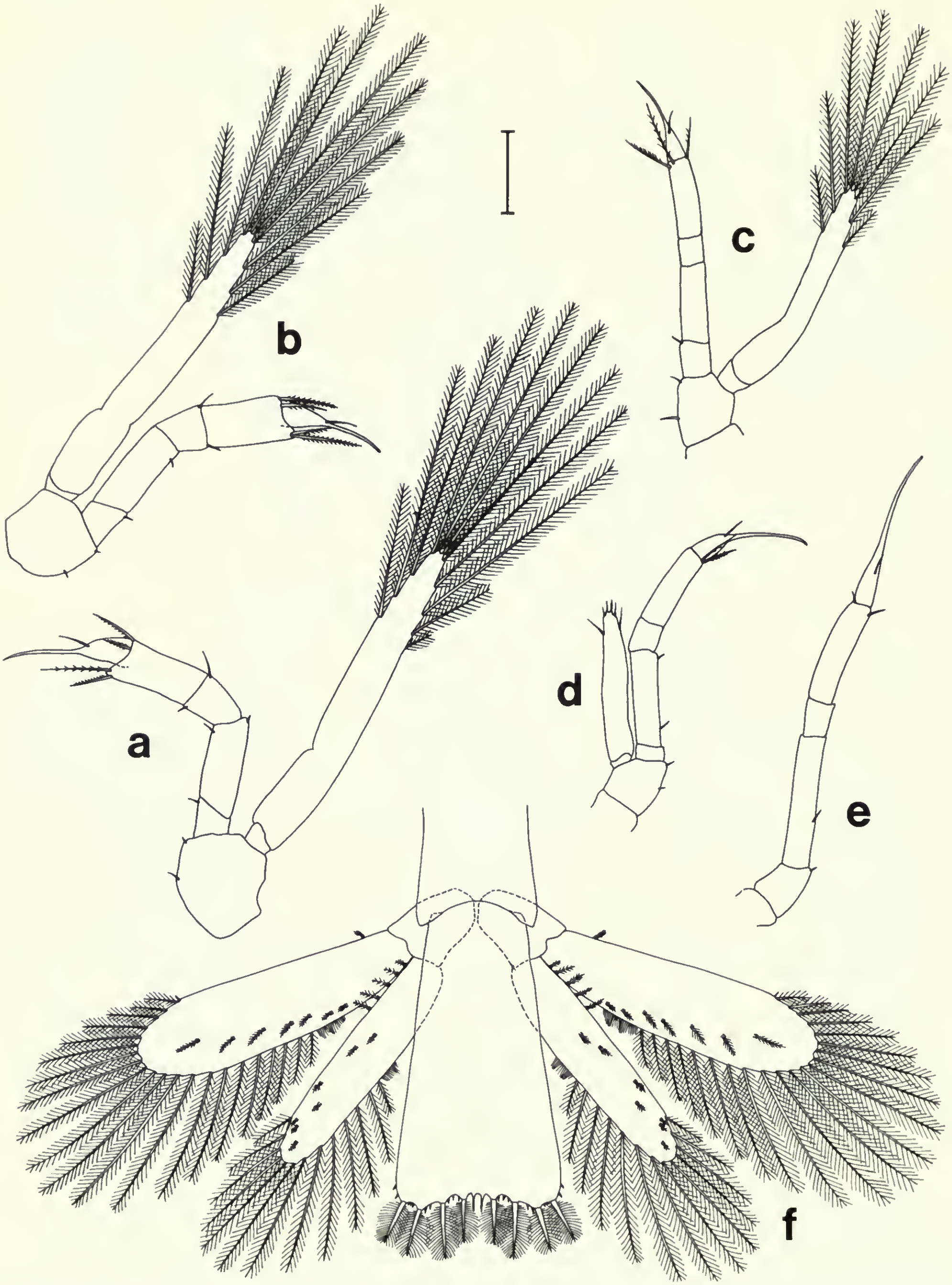

Fig. 9 Zoea 5: (a) pereiopod 1; (b) pereiopod 2; (c) pereiopod 3; (d) pereiopod 4; (e) pereiopod 5; (f) telson. Bar scale: 0·2 mm.

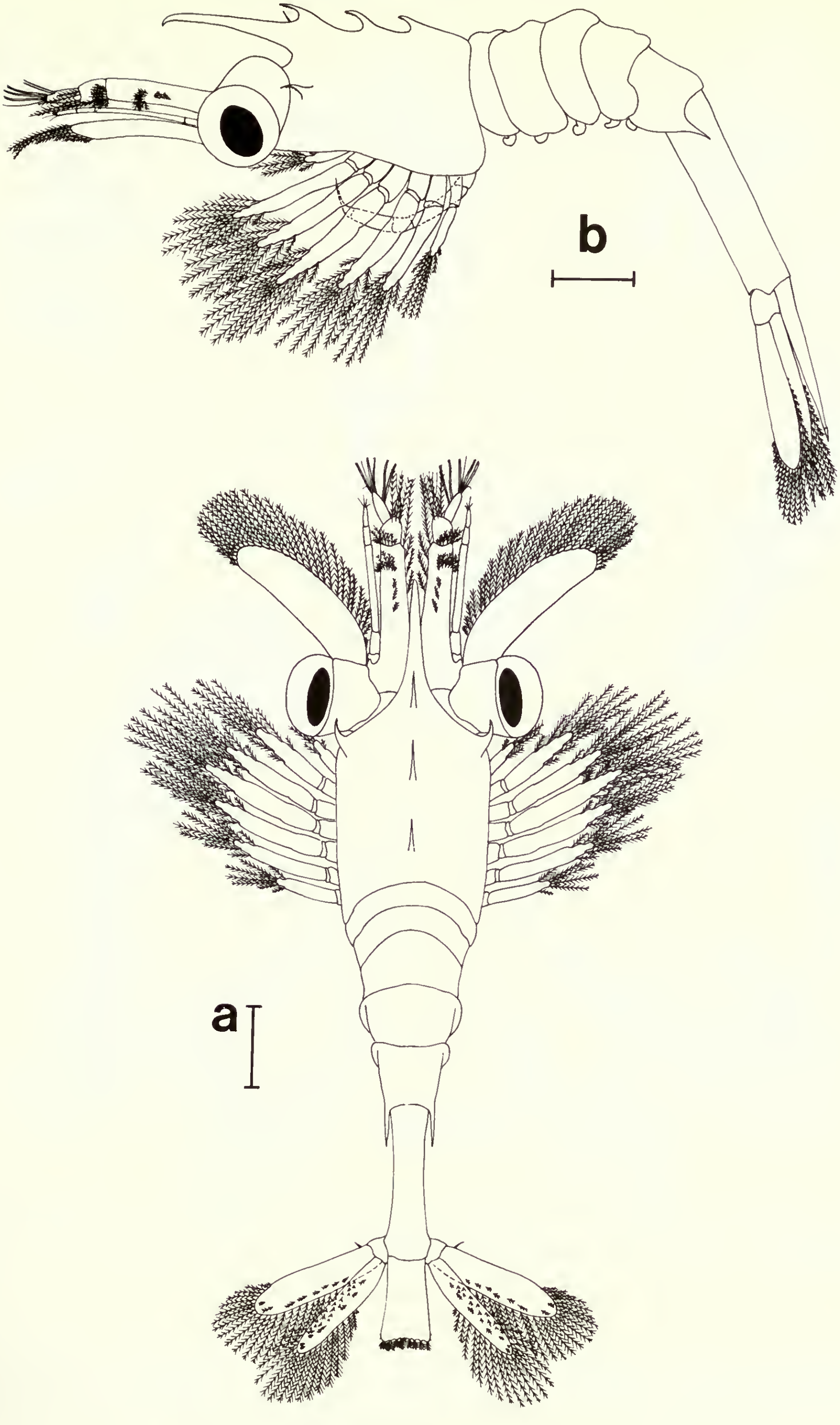

Fig. 10 Zoea 6: (a) dorsal view; (b) lateral view. Bar scales: 0·5 mm.

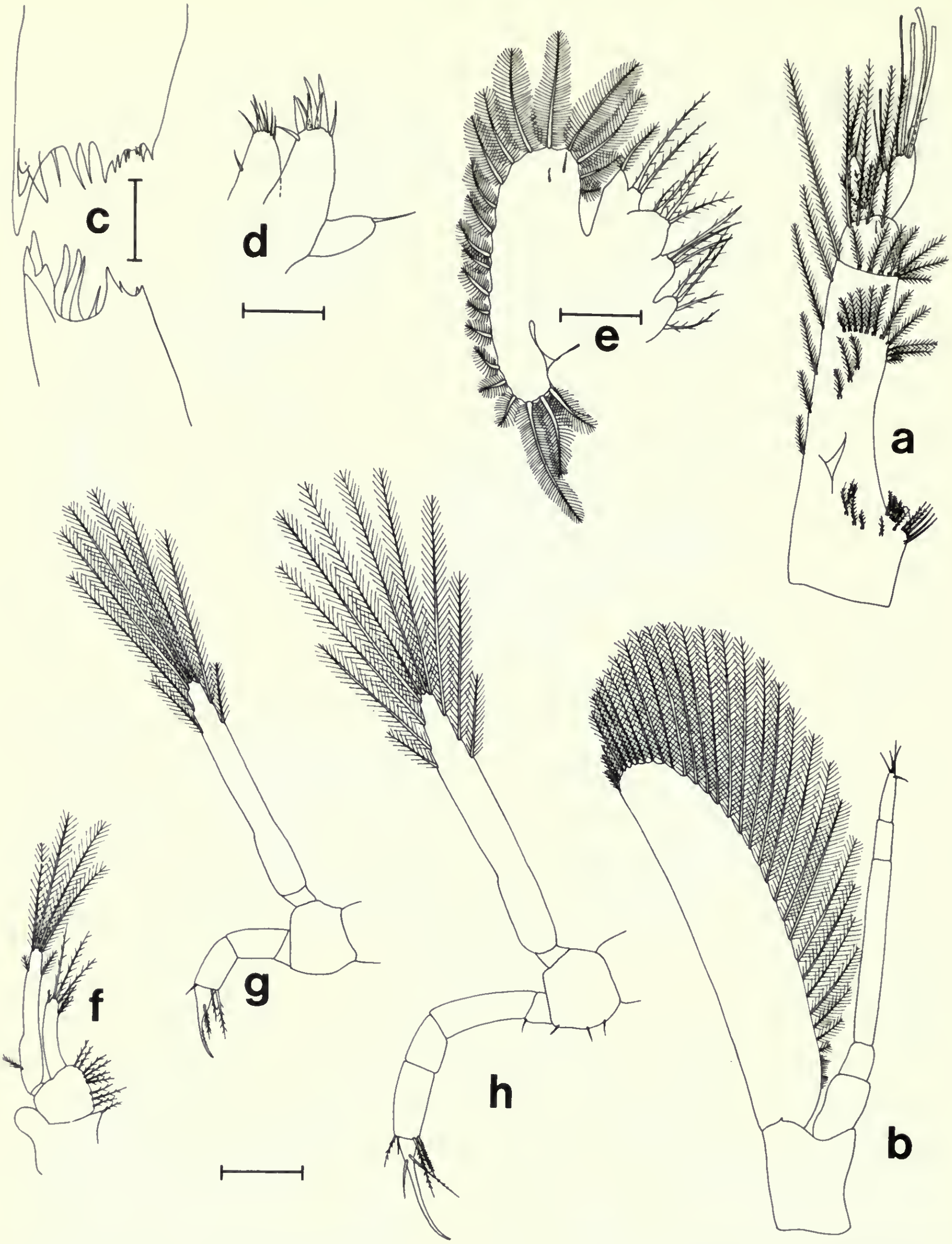

Fig. 11 Zoea 6: (a) antenna 1; (b) antenna 2; (c) mandibles; (d) maxilla 1; (e) maxilla 2; (f) maxilliped 1; (g) maxilliped 2; (h) maxilliped 3. Bar scales: a, b, f–h = 0·2 mm; c = 0·05 mm; d, e = 0·1 mm.

Pereiopod 4 (Figs 15d, e): exopodite occasionally with fringing plumose setae much reduced.
Abdomen (Figs 13b, 15g–k): pleopods 1–5 still rudimentary, biramous with traces of terminal setae on exopodites.
Telson (Figs 13a, 15l): *posterior margin straight or slightly convex.*

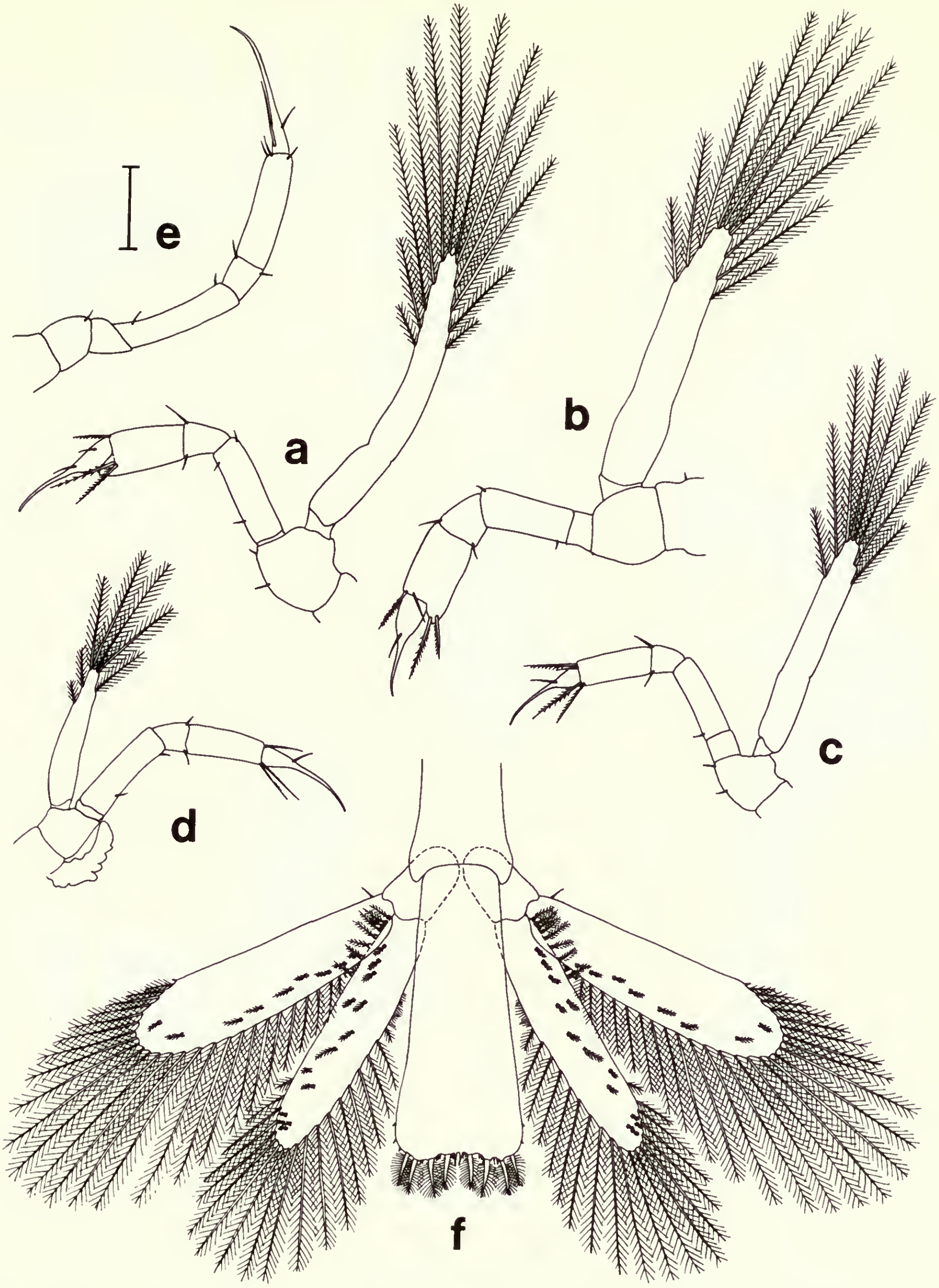

Fig. 12 Zoea 6: (a) pereiopod 1; (b) pereiopod 2; (c) pereiopod 3; (d) pereiopod 4; (e) pereiopod 5; (f) telson. Bar scale: 0·2 mm.

ZOEA 8 (Figs 16–19) 6·6 mm (5·8–7·1 mm)

Maxilliped 1 (Fig. 18a): *up to 6 plumose setae on proximo-lateral margin of exopodite.*
Pereiopod 1, 2 (Figs 18d, e): *endopodite with internal distal margin produced forward to over half length of dactylus* (excluding terminal setae).
Telson (Fig. 19i): *posterior margin convex.*

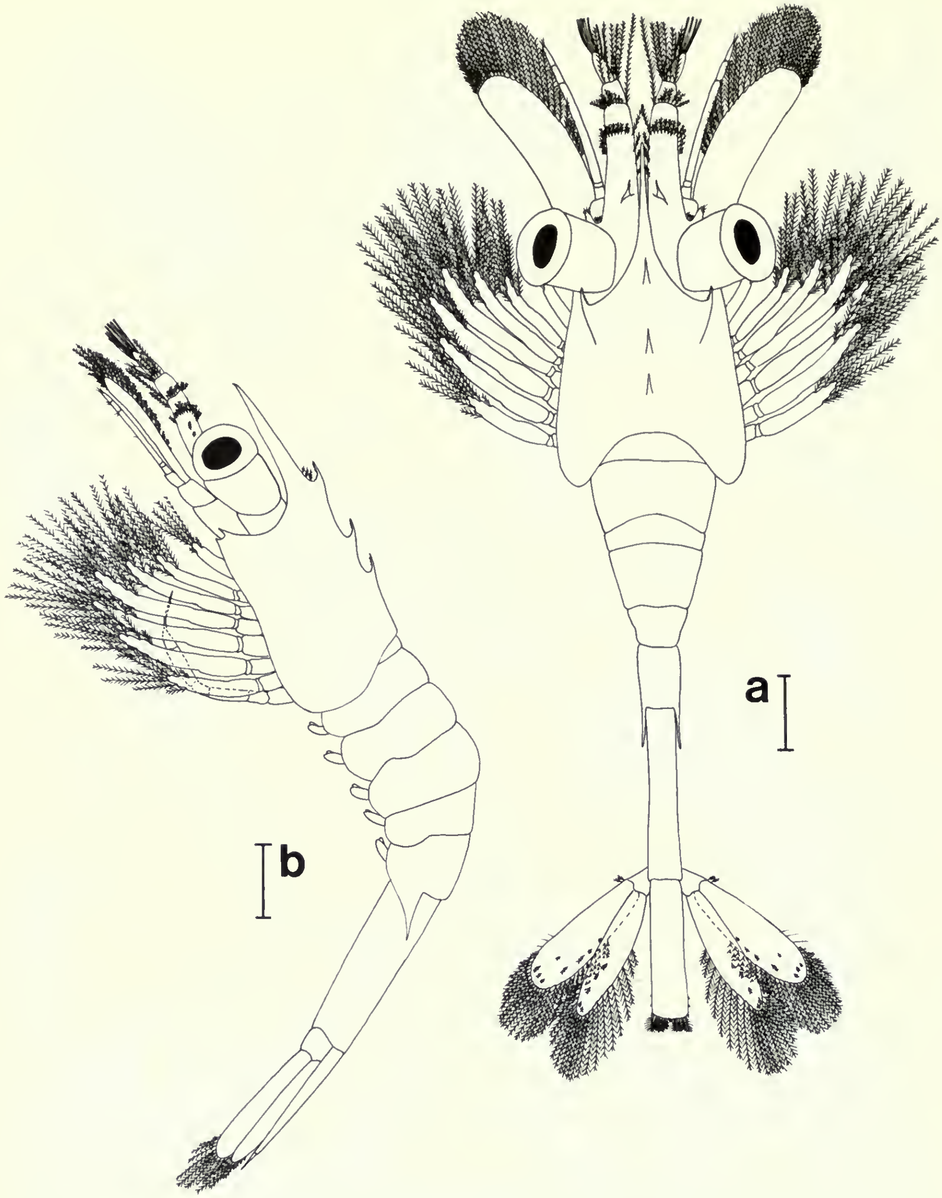

Fig. 13 Zoea 7: (a) dorsal view; (b) lateral view. Bar scales: 0·5 mm.

Zoea 9 (Figs 20–23) 7·3 mm (6·9–7·9 mm)

Carapace (Fig. 20b): *3 short plumose setae in angle of anterior dorso-medial spine, 1 in angle of second dorso-medial spine.*

Antenna 1 (Fig. 21a): internal flagellum of 1 or 2 segments, *external flagellum of 2 segments;* 3 or 4 groups of aesthetascs on internal margin of external flagellum; *statocyst fully developed.*

Antenna 2 (Fig. 21b): increase in number of segments of endopodite flagellum, *now longer than scathocerite.*

Maxilliped 1 (Fig. 21g): *14 to 20 setae on internal margin of basis, 5 to 9 plumose setae on proximo-lateral margin of exopodite.*

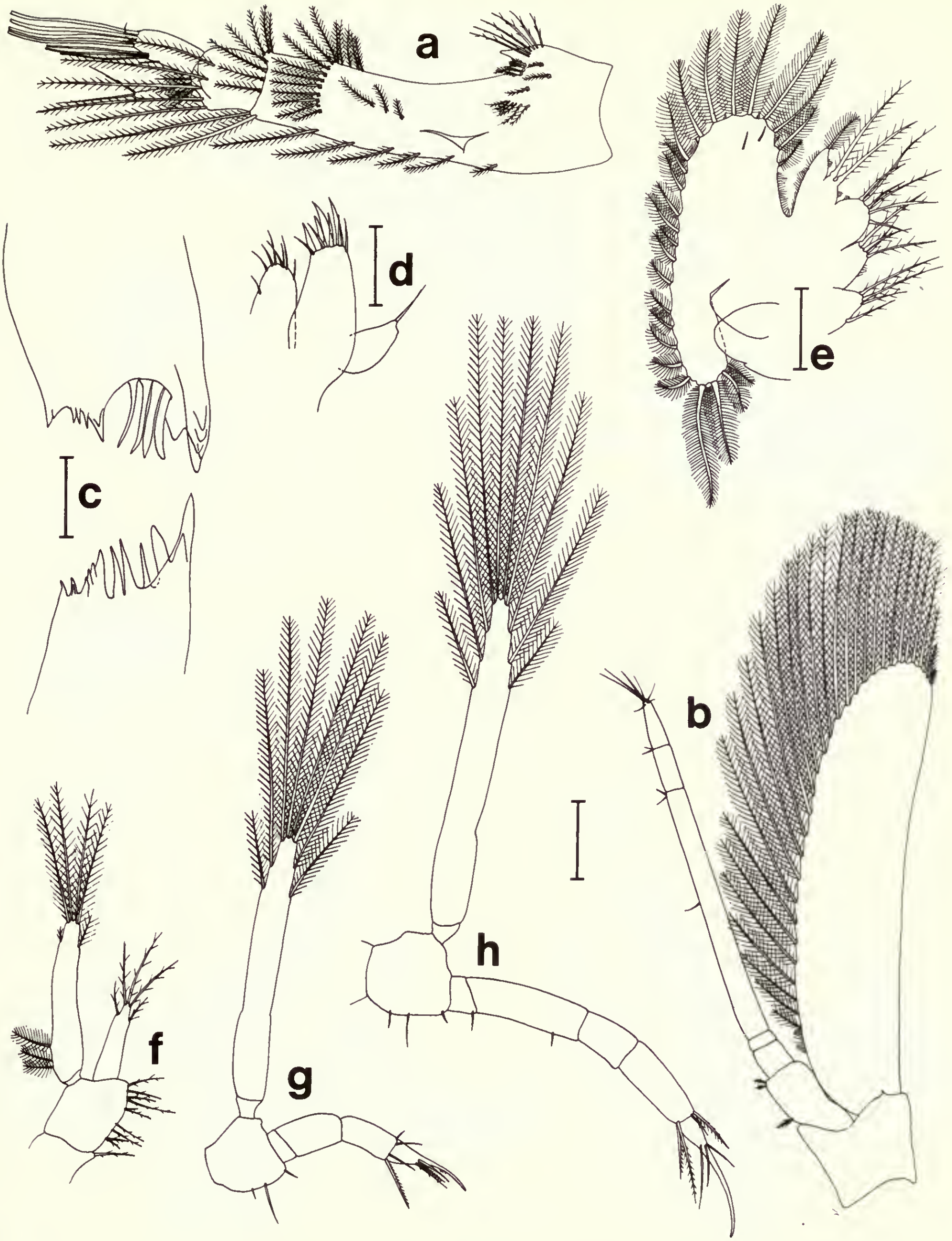

Fig. 14 Zoea 7: (a) antenna 1; (b) antenna 2; (c) mandibles; (d) maxilla 1; (e) maxilla 2; (f) maxilliped 1; (g) maxilliped 2; (h) maxilliped 3. Bar scales: a, b, f–h = 0·2 mm; c = 0·05 mm; d, e = 0·1 mm.

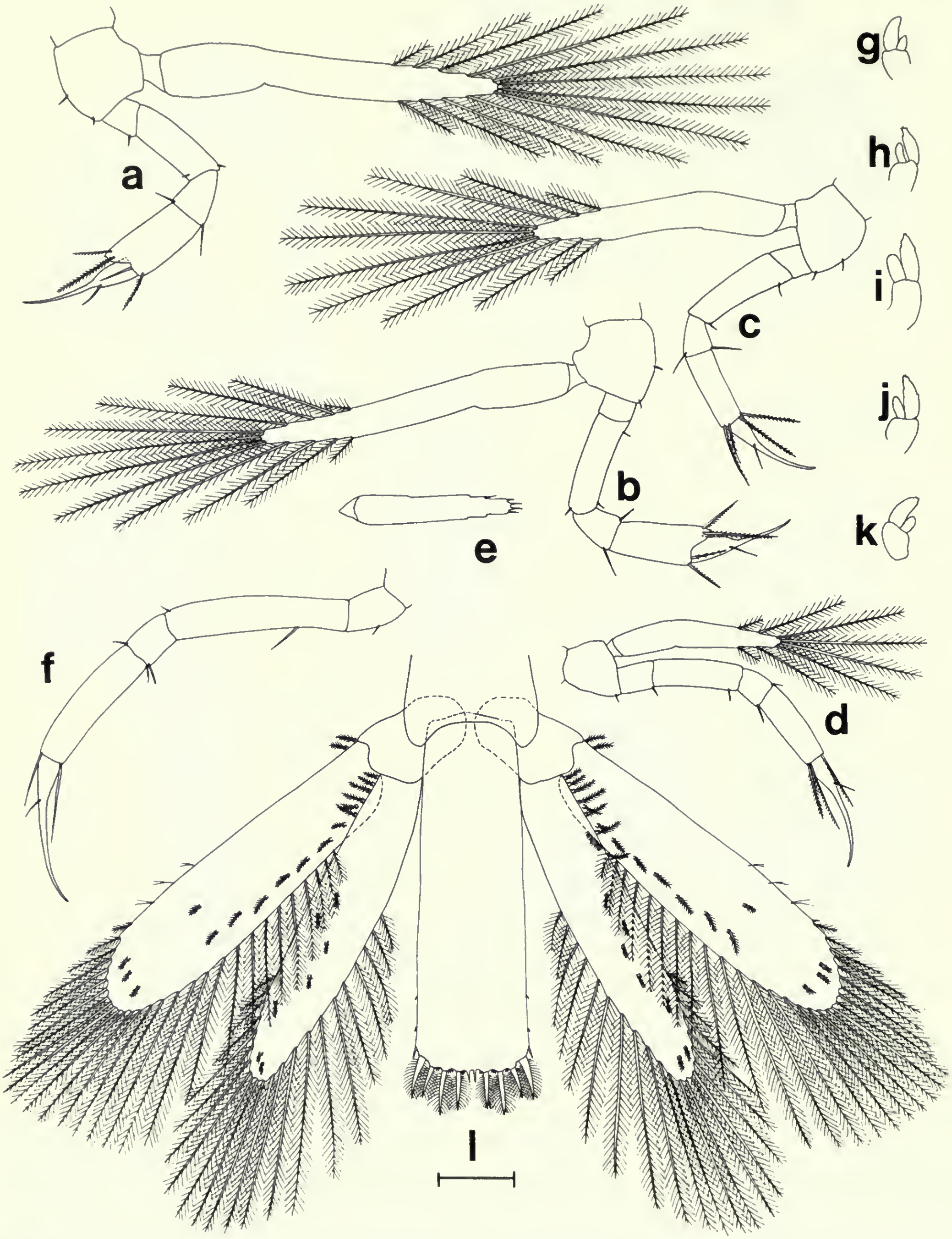

Fig. 15 Zoea 7: (a) pereiopod 1; (b) pereiopod 2; (c) pereiopod 3; (d) pereiopod 4; (e) variant of pereiopod 4 exopod with reduced setae; (f) pereiopod 5; (g) pleopod 1; (h) pleopod 2; (i) pleopod 3; (j) pleopod 4; (k) pleopod 5; (l) telson. Bar scale = 0·2 mm.

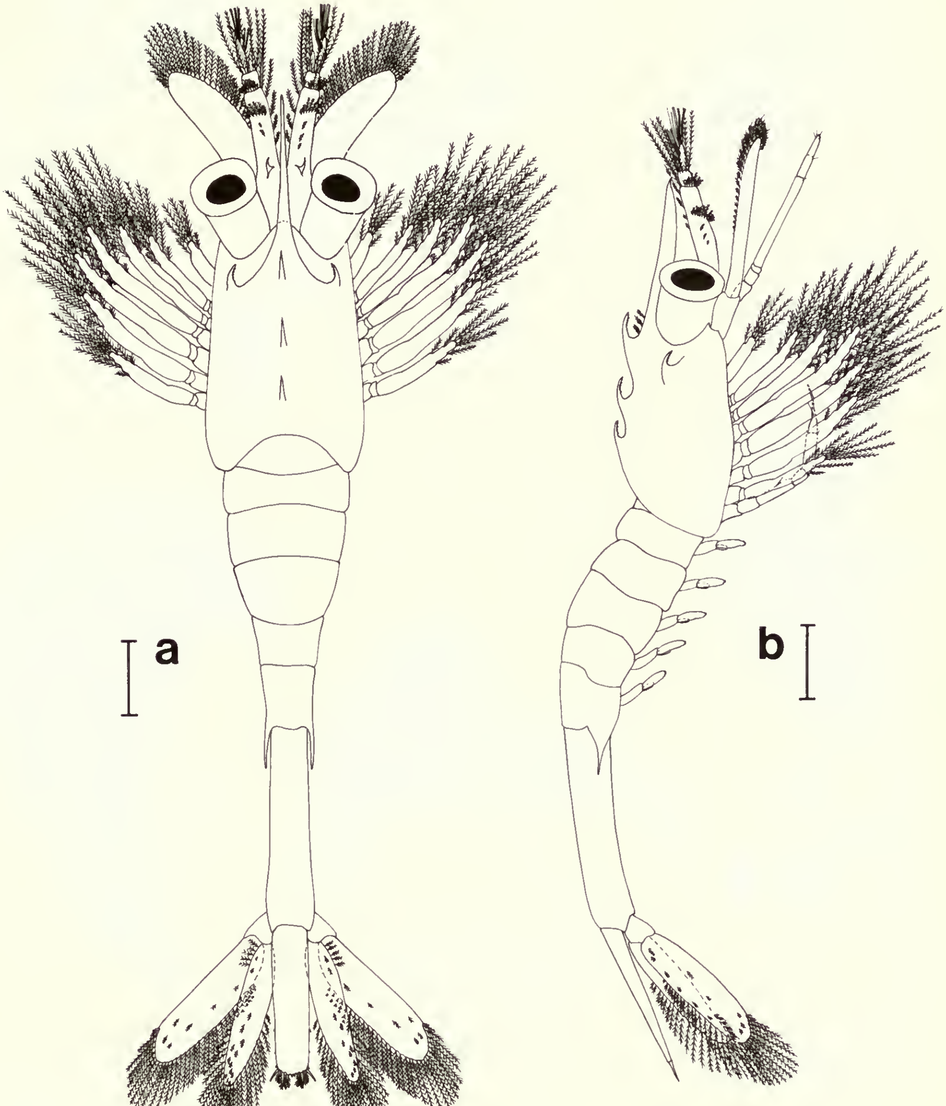

Fig. 16 Zoea 8: (a) dorsal view; (b) lateral view. Bar scales: 0·5 mm.

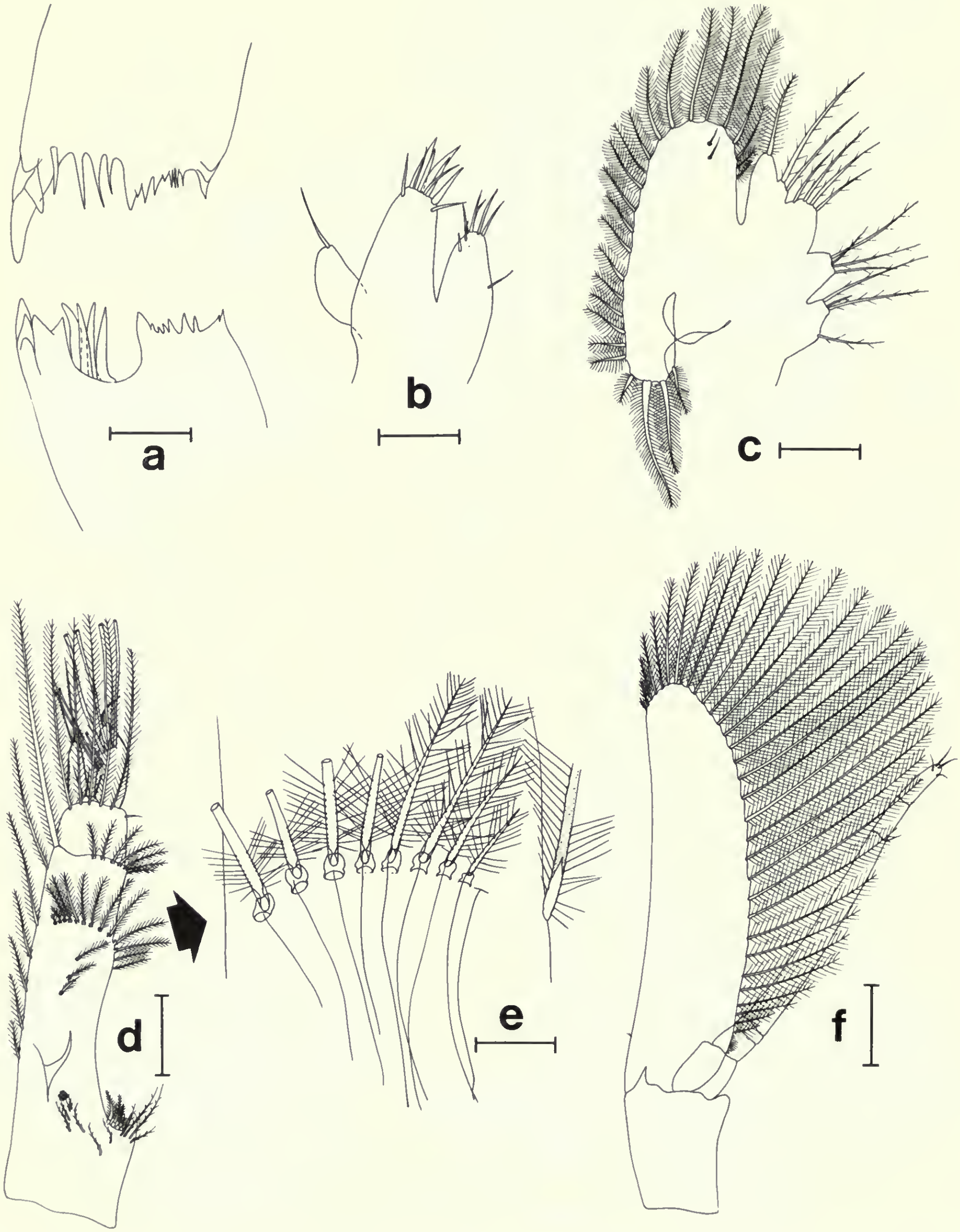

Fig. 17 Zoea 8: (a) mandibles; (b) maxilla 1; (c) maxilla 2; (d) antenna 1; (e) antenna 1 – enlargement of proximal array of sensory hairs showing thread-like connections remaining in cast exoskeleton; (f) antenna 2. Bar scales: a, e = 0·05 mm; b, c = 0·1 mm; d, f = 0·2 mm.

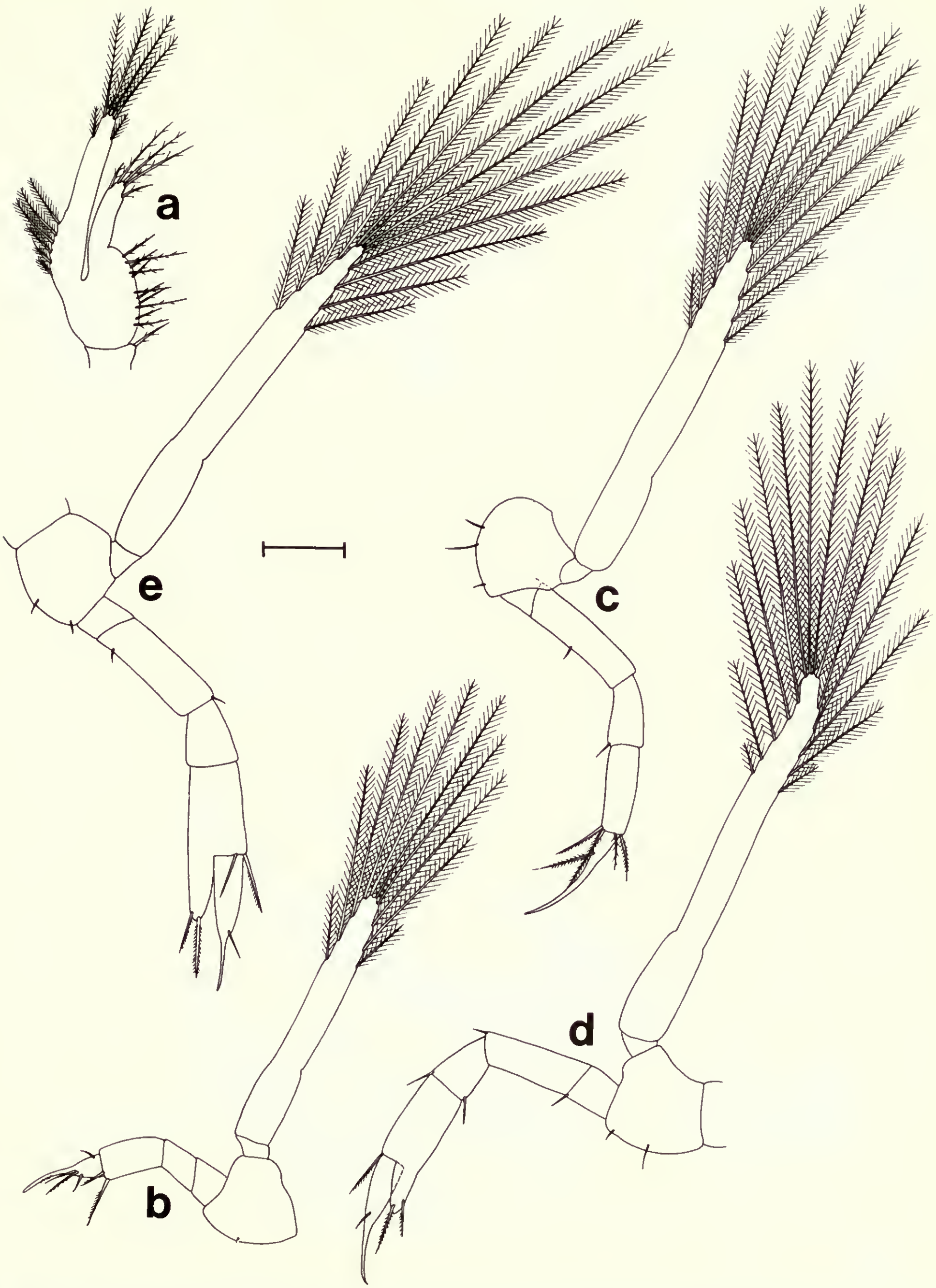

Fig. 18 Zoea 8: (a) maxilliped 1; (b) maxilliped 2; (c) maxilliped 3; (d) pereiopod 1; (e) pereiopod 2. Bar scale: 0·2 mm.

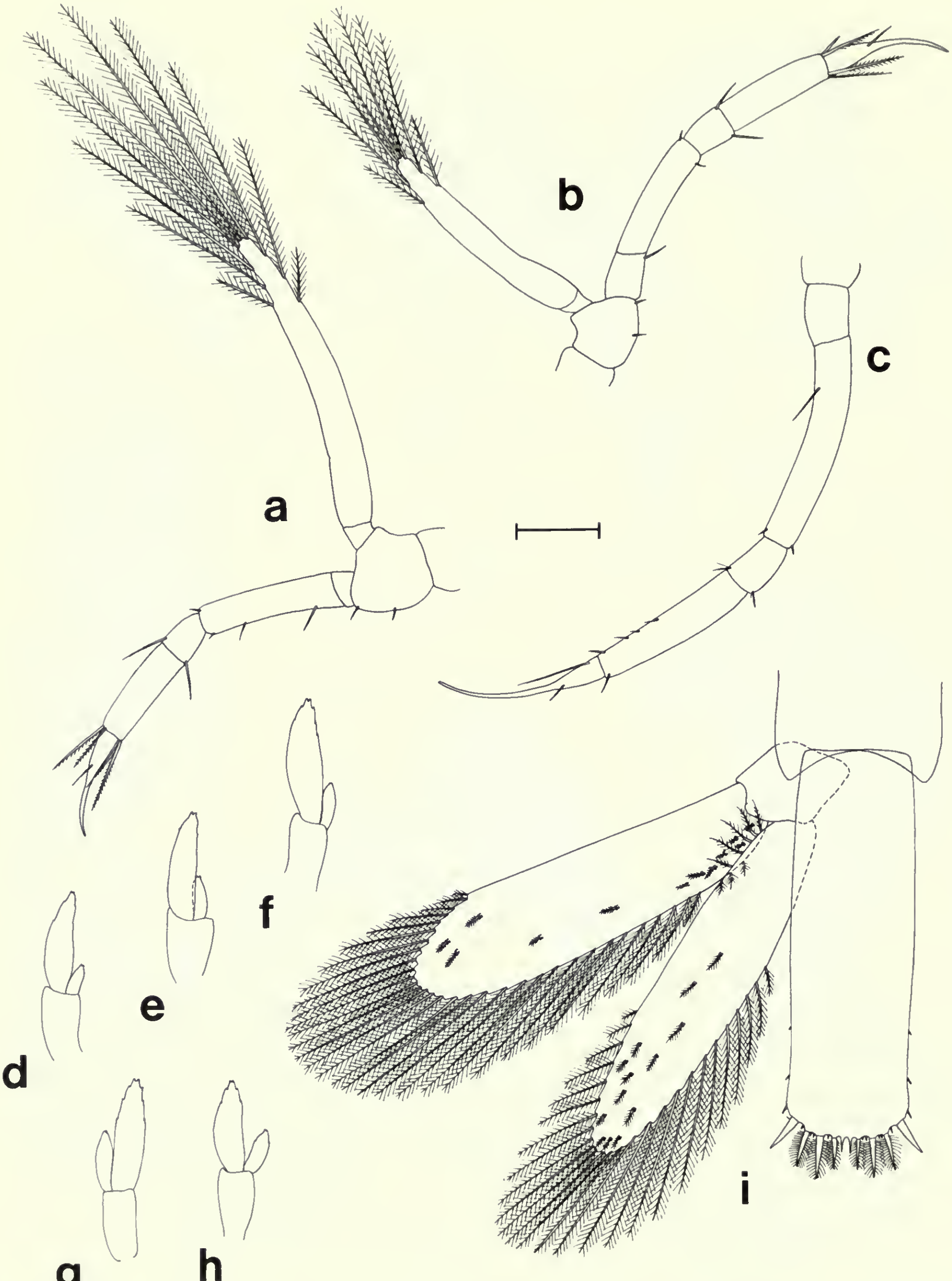

Fig. 19 Zoea 8: (a) pereiopod 3; (b) pereiopod 4; (c) pereiopod 5; (d) pleopod 1; (e) pleopod 2; (f) pleopod 3; (g) pleopod 4; (h) pleopod 5; (i) telson. Bar scale: 0·2 mm.

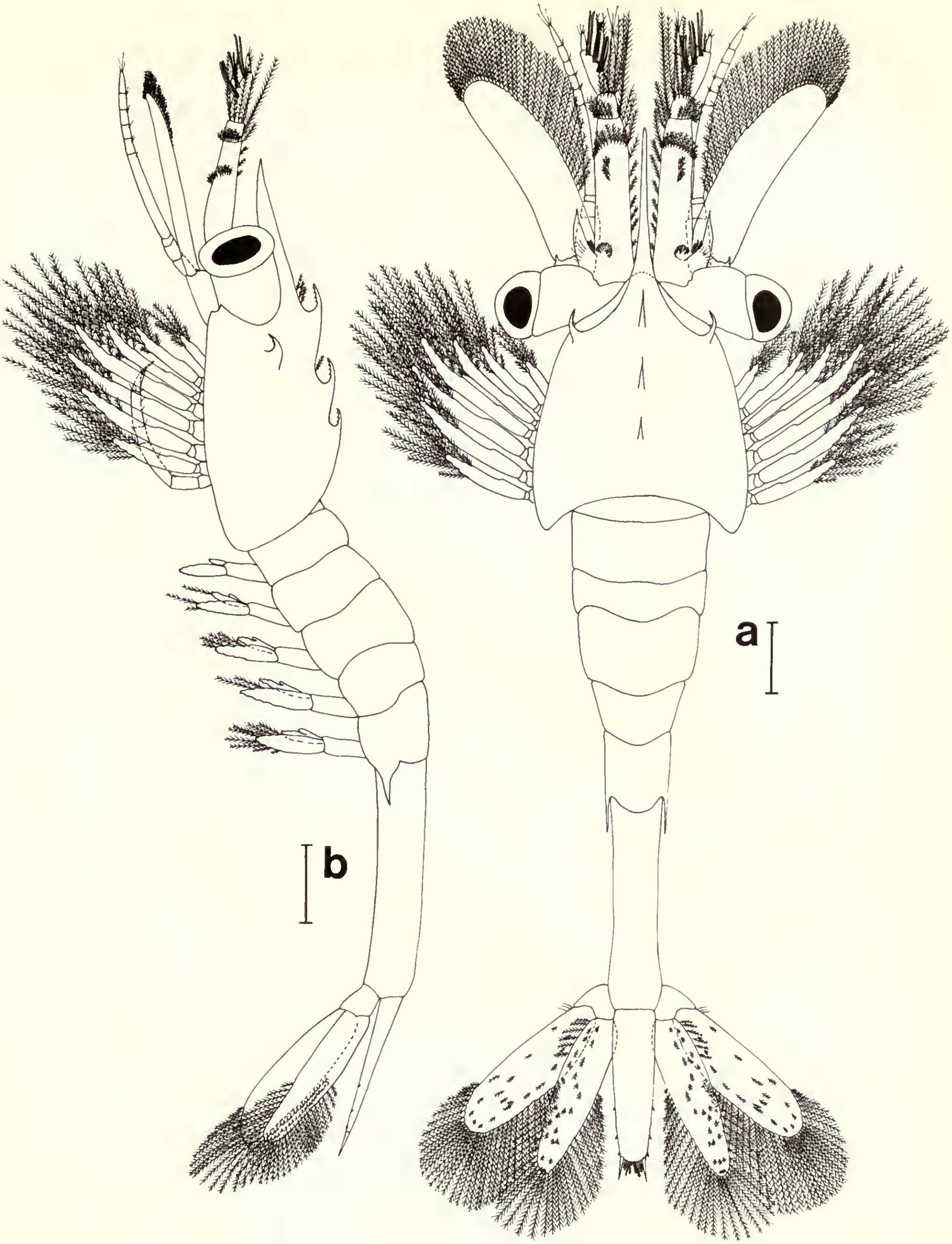

Fig. 20 Zoea 9: (a) dorsal view; (b) lateral view. Bar scales: 0·5 mm.

Pereiopods 1, 2 (Figs 22c, d): *endopodite with immovable finger of propodus produced forward to almost length of dactylus* (excluding terminal setae)
Abdomen (Figs 20b, 23c–g): *pleopods with rudimentary setae, a few fully plumose; endopodite of pleopods 2 to 5 with rudiment of appendix interna* (stylamblys).
Telson (Fig. 23h): *further narrowing distally, posterior margin with 4+4 large spines (no small spines between)* and with 3 reduced spines on latero-distal margin.

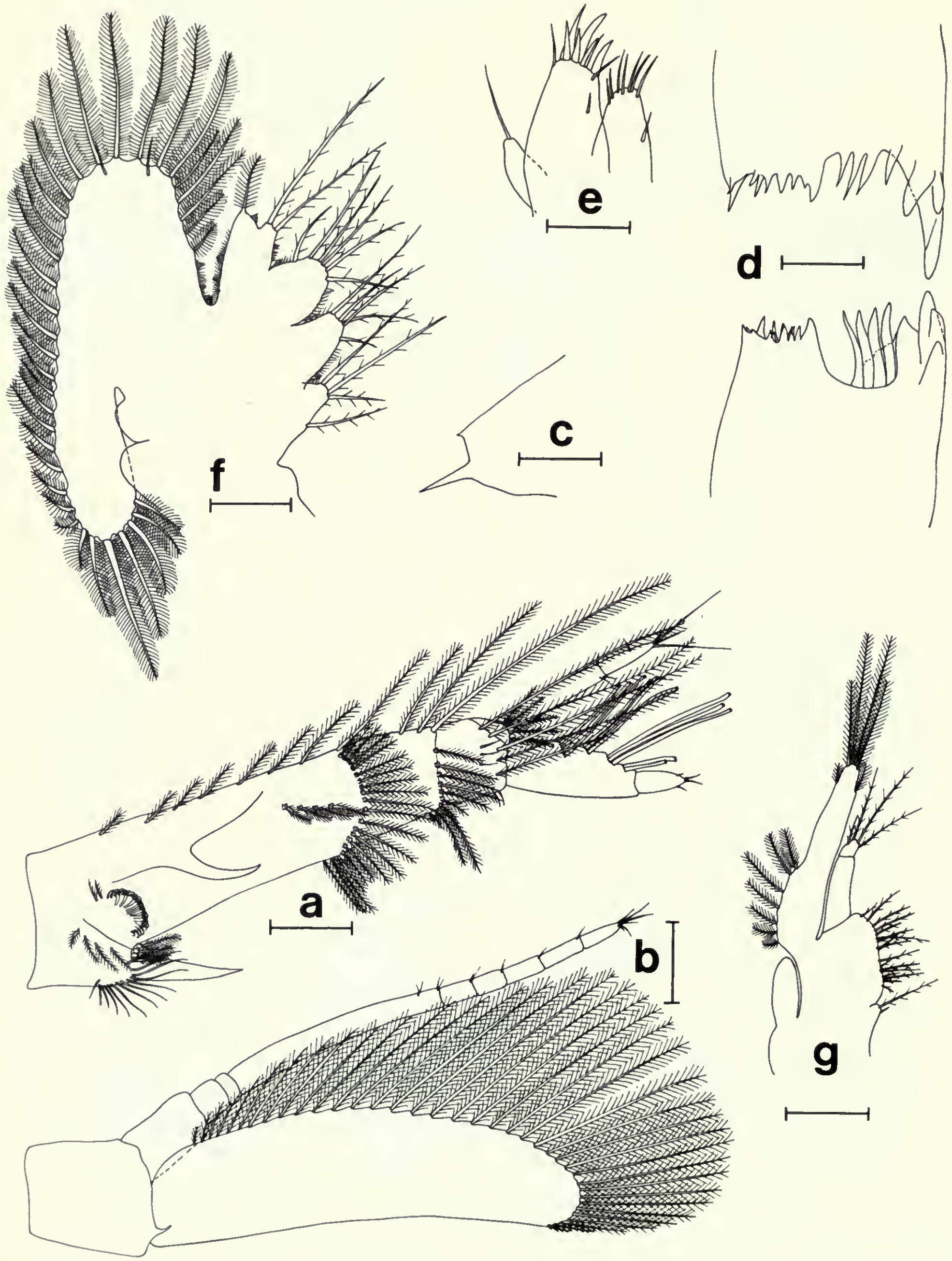

Fig. 21 Zoea 9: (a) antenna 1; (b) antenna 2; (c) antero-lateral teeth of carapace; (d) mandibles; (e) maxilla 1; (f) maxilla 2; (g) maxilliped 1. Bar scales: a, b, g = 0·2 mm; c, d = 0·05 mm; e, f = 0·1 mm.

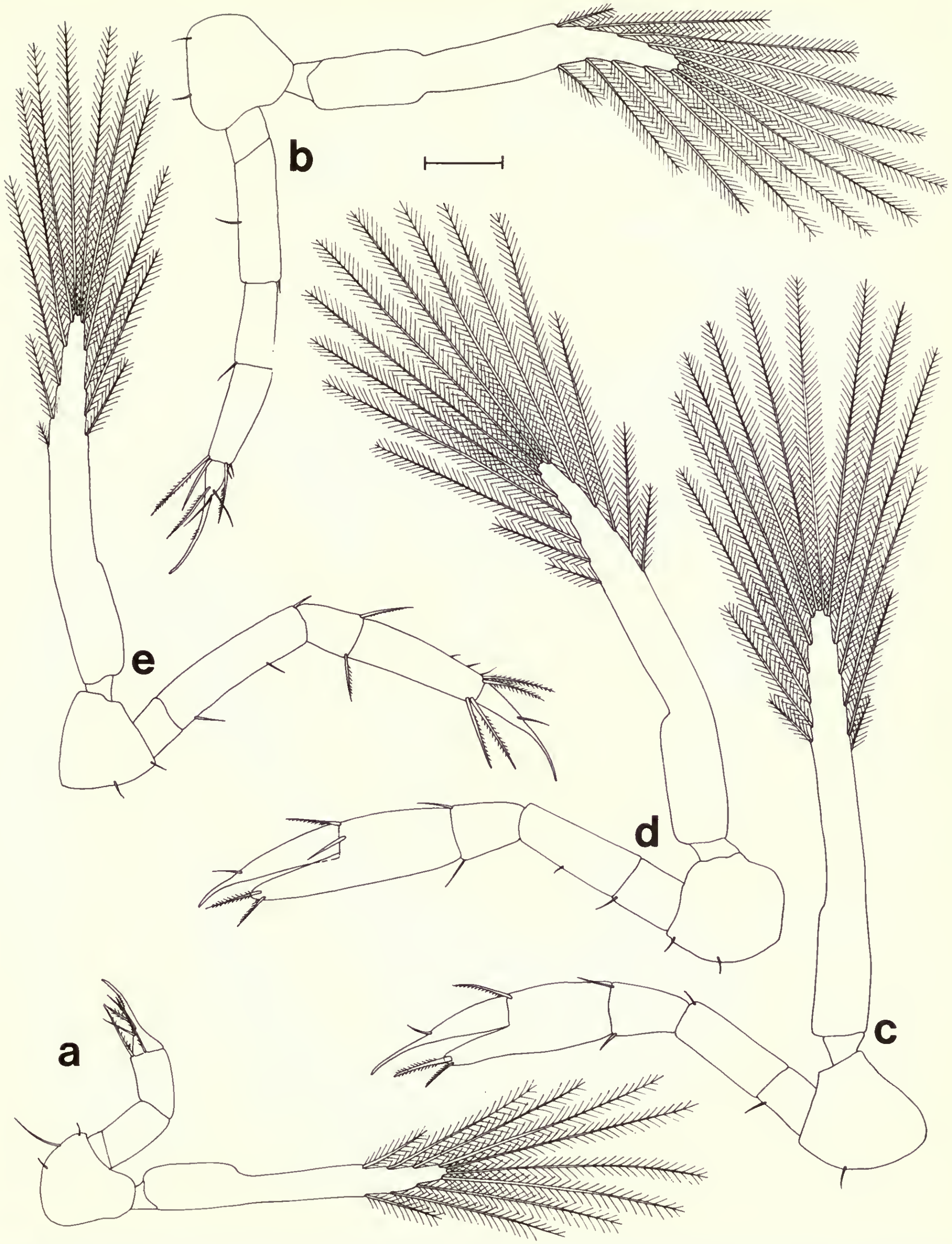

Fig. 22 Zoea 9: (a) maxilliped 2; (b) maxilliped 3; (c) pereiopod 1; (d) pereiopod 2; (e) pereiopod 3. Bar scale = 0·2 mm.

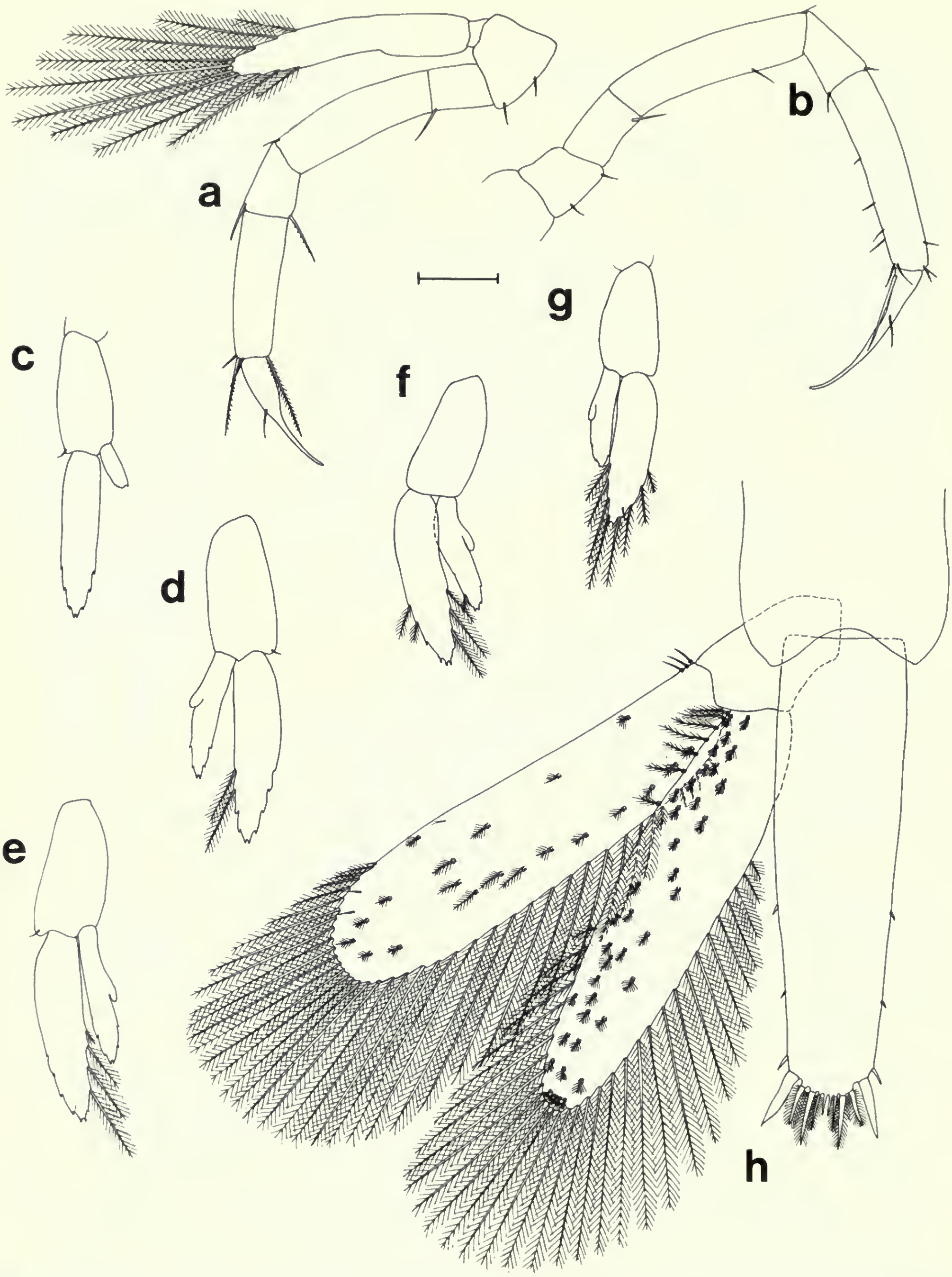

Fig. 23 Zoea 9: (a) pereiopod 4; (b) pereiopod 5; (c) pleopod 1; (d) pleopod 2; (e) pleopod 3; (f) pleopod 4; (g) pleopod 5; (h) telson. Bar scale: 0·2 mm.

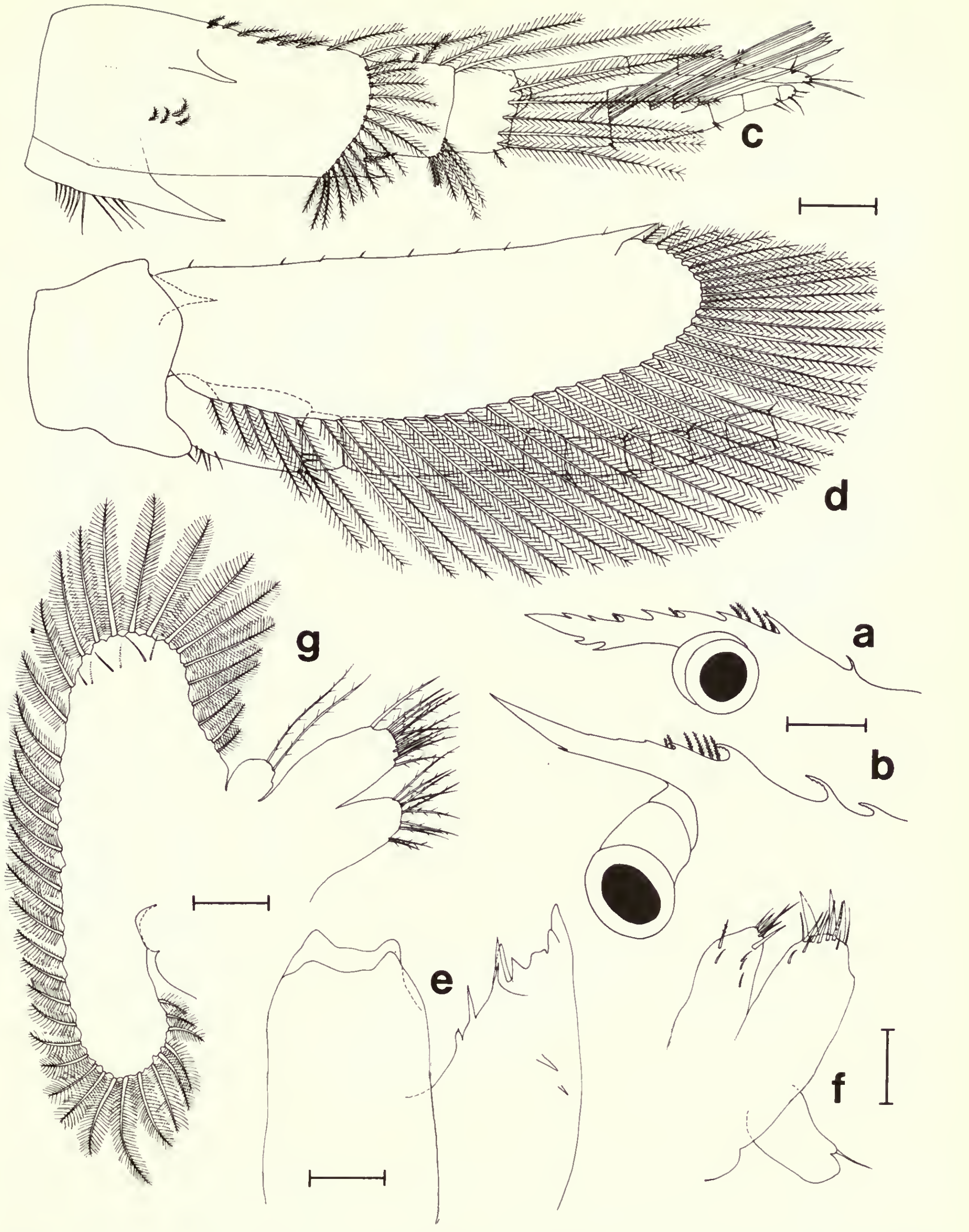

Fig. 24 Post larva 1: (a) rostrum; (b) rostrum with characters intermediate between larval and post larval phases; (c) antenna 1; (d) antenna 2; (e) mandible; (f) maxilla 1; (g) maxilla 2. Bar scales: a, b = 0·5 mm; c, d = 0·2 mm; e = 0·05 mm; f, g = 0·1 mm.

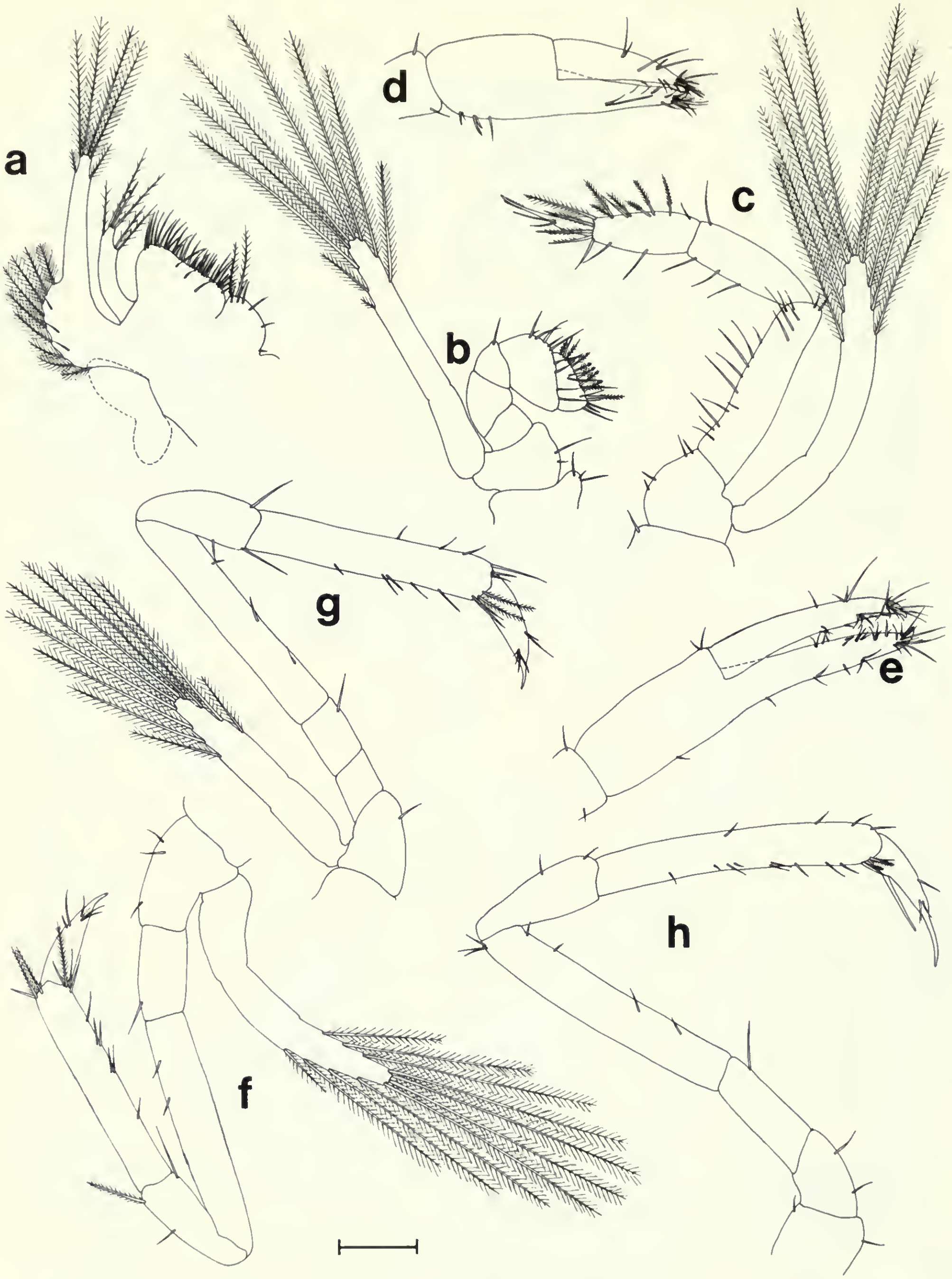

Fig. 25 Post larva 1: (a) maxilliped 1; (b) maxilliped 2; (c) maxilliped 3; (d) pereiopod 1 chela; (e) pereiopod 2 chela; (f) pereiopod 3; (g) pereiopod 4; (h) pereiopod 5. Bar scale: 0·2 mm.

Post larva 1 (Figs 24–26) 7·9 mm (7·0–8·6 mm)
Most specimens had metamorphosed to post larvae or intermediate stages at this moult. Meristic characters of the more advanced individuals are described here and included in Table 1.

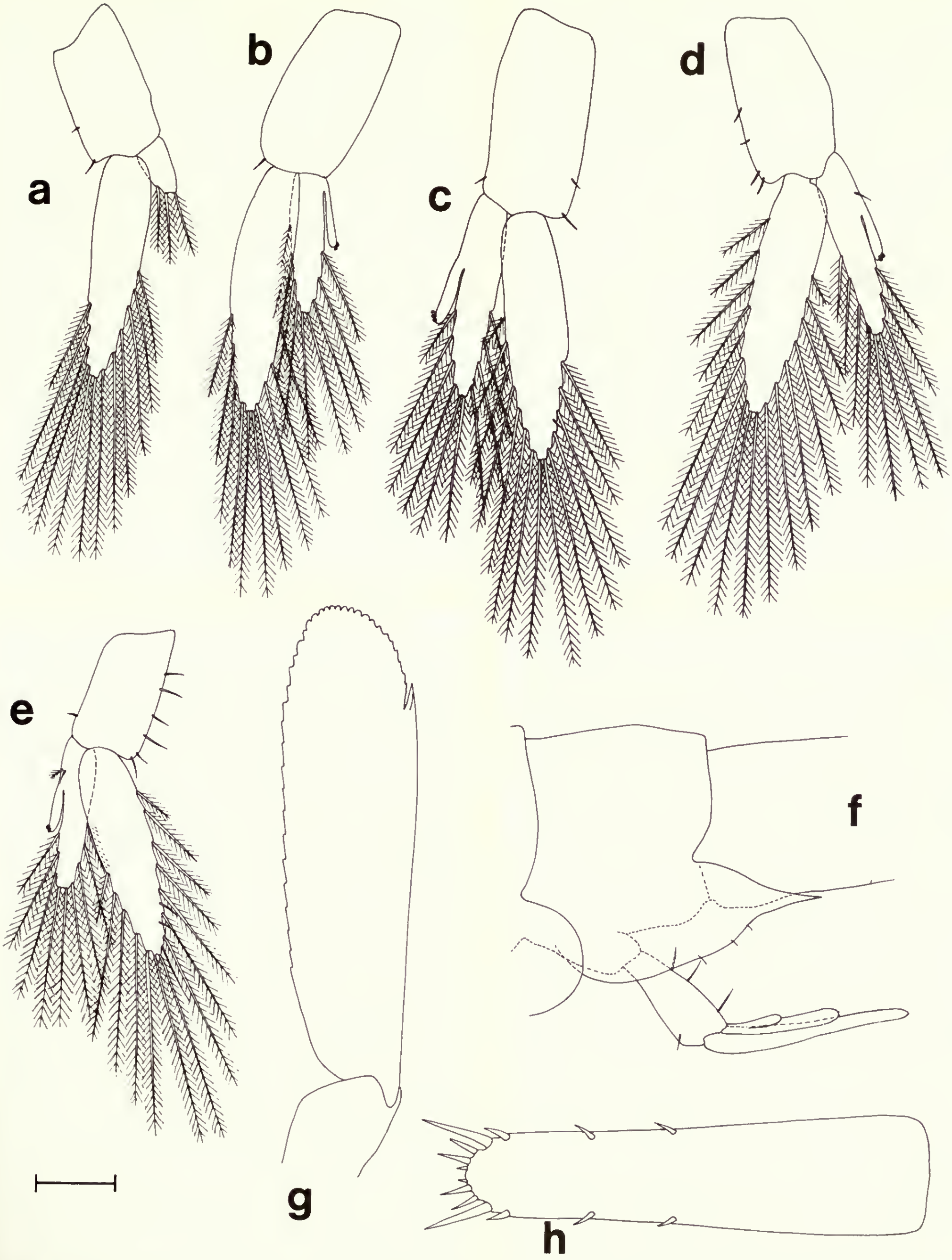

Fig. 26 Post larva: (a) pleopod 1; (b) pleopod 2; (c) pleopod 3; (d) pleopod 4; (e) pleopod 5; (f) somite 5 with postero-lateral spines (plumose setae of pleopod 5 not shown); (g) uropod exopodite (plumose setae not shown); (h) telson. Bar scale: 0·2 mm.

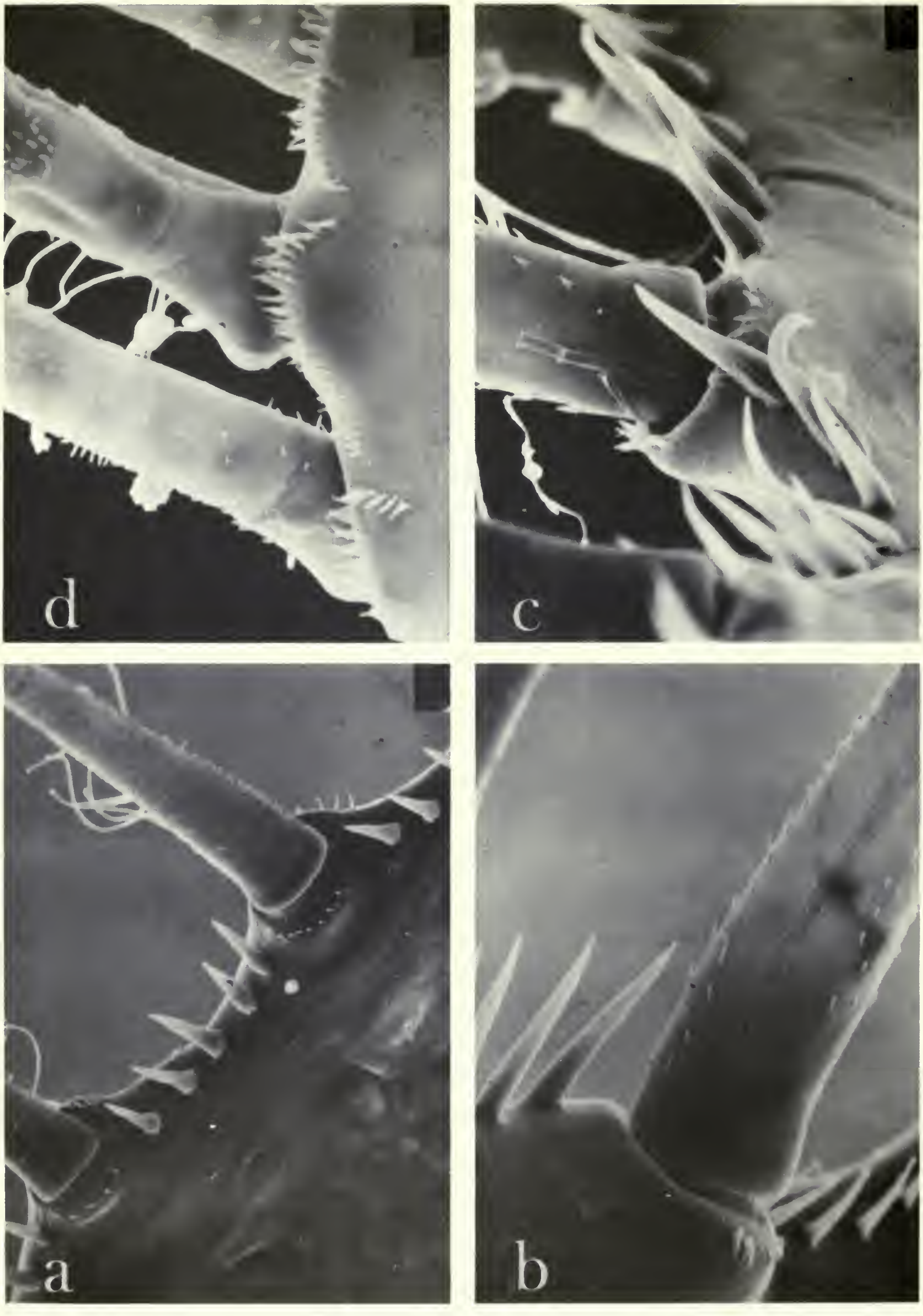

Fig. 27 Telson of palaemonid Zoea 1. (a) Dorsal view of posterior margin. Bases of large plumose spines with row of smaller spines between. (b) Single large spine ornamented with spinules. (c) Articulation at base of large spines with circlet of small spines. (d) Ventral view of posterior margin showing rows of small spines arranged with gaps.

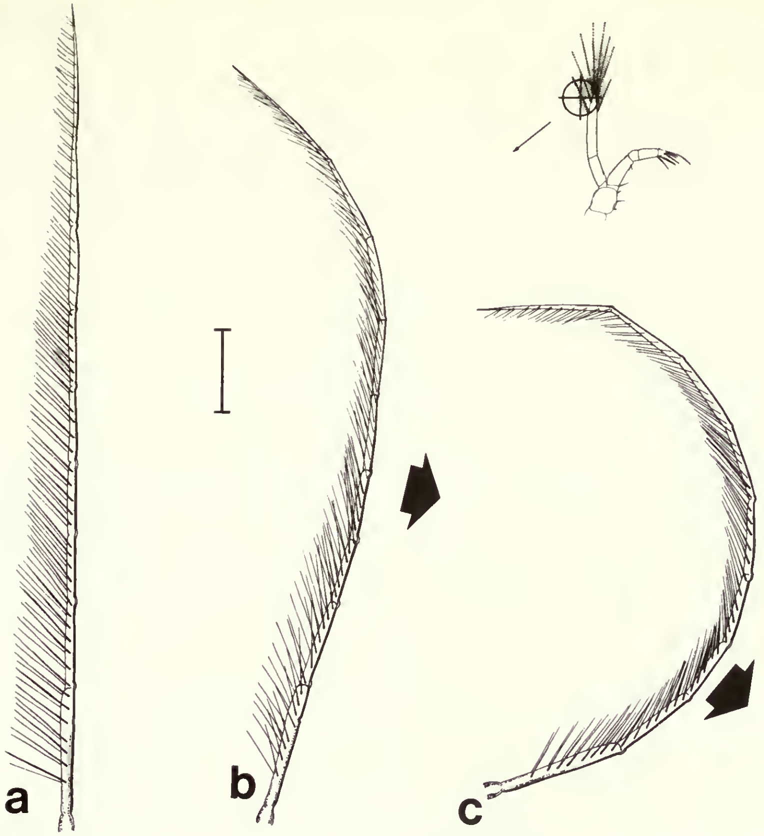

Fig. 28 Single plumose seta from natatory exopodite of pereiopod. Shaft is a differentially thickened cylinder hinged at intervals and bears two rows of thin lateral setules. (a) Seta stationary. (b) Beginning of recovery stroke. (c) End of recovery stroke. Bar scale: 0·05 mm.

Carapace (Fig 24a): *rostrum with 6 or 7 dorsal and 2 ventral teeth,* rostral tip straight. *Supra-orbital spines missing.* Intermediate condition of rostrum shown in Fig. 24b.

Antenna 1 (Fig. 24c): *internal flagellum of 5 or more segments and external flagellum of 6 or more segments.*

Antenna 2 (Fig. 24d): endopodite multisegmented, at least twice as long as scaphocerite.

Mandible (Fig. 24e); *divided into pars incisiva and pars molaris,* lacinia mobilis no longer present and palp (three jointed in adult) not yet appeared.

Maxilla 2 (Fig. 24f): reduction of setae on coxal endite and endopodite, increase in setae on basal endites.

Maxilliped 2 (Fig. 25b): endopodite with dactylus, propodus and merus flattened.

Maxilliped 3 (Fig. 25c): endopodite dactylus shortened.

Pereiopods 1, 2 (Figs 25d, e): *immovable finger of propodus same length as dactylus.*

Pereiopods 3, 4 (Figs 25f, g): dactylus shortened.

Pleopod 1 (Fig. 26a): *ratio of endopodite to exopodite 1:4;* endopodite bearing terminal plumose setae, exopodite fringed with long plumose setae.

Pleopods 2–5 (Figs 26b–e): endopodite over half length of exopodite, both with long, marginal plumose setae, endopodite with appendix interna bearing well developed intero-distal coupling hooks.

Abdomen (Fig. 26f): fifth abdominal somite with posterior margin still produced into pair of lateral spines.

Telson (Fig. 26g): intermediate condition (extreme narrowing with posterior margin tapering to point not yet developed).

Discussion

Most of the specimens reared by Sollaud (1912) at the Marine Laboratory in Roscoff reached metamorphosis after 8 larval stages. But he found also '... quelques individus, en effet, peuvent présenter un stade IX supplementaire avant de se transformer...' He concluded, however, that the normal larval development for *Palaemon serratus* was eight stages (Sollaud, 1923). In the present work the differences between stages 8 and 9 were slight and confirm, therefore, the conclusion reached by Sollaud. The insertion of extra moults which probably represents an adaptation to sub-optimal conditions by prolonging larval existence is a recurrent feature of the development of Palaemoninae (Fincham, 1977, 1979). Sandifer and Smith (1979) indicated that in addition to being affected by environmental factors the tendency of individual palaemonid larvae to pass through a given number of larval stages may be inherited. They suggested also that variation in development may enhance the general advantages of an extended planktonic larval phase, a common feature of 'r' strategists. These include greater potential for dispersion and the ability to colonize new habitats quickly if favourable conditions occur. A variable planktonic existence may produce a wider spread of individuals of a given brood and average the risks of survival. At the population level Sandifer and Smith emphasize that early metamorphosis will enhance the possibility of gene flow between populations.

Many environmental factors affect development including photoperiodicity. Wickins (1972) reported work on larval *Palaemon serratus* in which growth was improved and metamorphosis reached sooner in those reared in continuous light. Eight hours dark and 16 hours light produced improved growth compared with 8 hours light and 16 hours dark; continuous darkness produced slowest growth and development. Dalley (1979) working with *Palaemon elegans* concluded that greatly increased mortality during larval development in non-circadian light regimes was due to desynchronization of the circadian rhythms of metabolic processes.

One feature commonly found in exuviae of the various larval stages are thin strands extending from the bases of sensory hairs (see Figs 17d, e). In a paper on the ultrastructure of the antennal sensilla of the shrimp *Acetes* Ball & Cowan (1977) describe dense strands of unknown composition crossing the base of their type 1 seta, which they consider uninnervated. Tracts leading from the bases of their other four types of seta contain axons. The exact nature of the strands in the exuviae of *Palaemon serratus* is not clear and will be examined further.

Swimming: adaptations and a mechanism

When palaemonid larvae first hatch they usually swim upside down and telson first. At rest the larvae tend to sink and there are several adaptations which slow the rate of descent. At either end of the body plumose setae or spines increase drag. Fringing plumose setae effectively double the area of the broad exopodite (scaphocerite) of antenna 2 at the anterior end of the body (Figs 1a, 2a, 3a, 5a, 7a, 10a, 13a, 16a, 20a). These antennal setae are thickened at the base (Fig. 4c) and their rigidity increases drag when the exopodites are spread.

At the posterior end the telson bears stout spines which are ornamented with rows of small spines and are also plumose (Figs 27a–d). The function of the ornamentation is uncertain but might further slow the rate of sinking. Body size increases as larval development progresses and the importance of even the large spines on the telson for increasing drag, diminishes when the sixth abdominal segment develops its appendages. The exopodites of these uropods appear at zoea 3 (Fig. 41) and endopodites at zoea 4 (Fig. 6k) and are broad and flat and fringed with plumose setae. The spreading of these uropods slows the rate of sinking during periods when the larva is not swimming.

The telson, however, retains its important function as a stabilizing hydrofoil throughout larval life and is supplied with powerful muscles that enable it to assist in orientation control. Its gradual transformation from a triangular shape at zoea 1 with a 7+7 spine formula (Figs 1m, 27a–d) to the narrow shape at the last larval stage with spine formula 4+4 and three pairs of lateral spines (Fig. 23h) accompanies the gradual development of more thoracic natatory exopodites.

In the present rearing programme food is supplied to the larvae in the form of *Artemia* nauplii. In the wild it is likely that copepods and other small planktonic organisms form the main source of food (Sollaud used copepods in his rearing work at Roscoff). The pursuit of prey – *Artemia* or copepods – necessitates accurate orientation and direction control. The propulsive locomotory force is provided by the natatory exopodites developed sequentially. Zoea 1 has only three natatory exopodites – those of the maxillipeds – but biramous pereiopods are developed later and are also integrated into a regular beating pattern of the limbs. Pereiopod 5 is in fact developed by stage 4 before pereiopod 4 in *Palaemon serratus* but has no exopodite and is therefore not involved in larval swimming. The effective area of the propulsive exopodites is extended by the fringing plumose setae. Preliminary analysis of the swimming action from cine film shows that there is a power stroke and a recovery stroke. The morphological adaptations of these plumose setae and their role in swimming behaviour was determined following the routine examination by light microscopy of hundreds of moults during the course of the rearing programme.

The shaft of the plumose setae fringing the natatory exopodites is a differentially thickened cylinder with flexible cuticular hinges at intervals along its length (Fig. 28a). The hinges only permit bending towards the unthickened side of the shaft. During the propulsive power stroke the setae remain straight with the two rows of thin, lateral setules set at an obtuse angle to the shaft, thus providing maximum surface area and purchase in the water. On the recovery stroke the flexible exopodite bends and the marginal plumose setae fold back along the many hinge lines with their thin side branches streaming out behind. This offers the least possible resistance by the exopodite to the water and repositions the limb ready to begin the next power stroke.

The rhythmic beating of the six pairs of setose thoracic exopodites in the three larval stages, and swimmerets or pleopods in the post larvae of lobsters, has been analysed from cine film by Neil *et al.* (1976), Macmillan *et al.* (1976) and Laverack *et al.* (1976). No comparable study has been made for a caridean with regular sequential addition of limbs (in lobsters all limbs are present on hatching). The rarity of palaemonid larvae in the plankton remains an enigma especially as they are apparently so well adapted for swimming. Detailed analyses of cine film of swimming in larval palaemonids, together with plankton sampling using a static bottom net and experimental work on the periodicity of larval swimming, all of which are in progress, should shed some light on the problem.

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The larval development of the Angular Crab, *Goneplax rhomboides* (Linnaeus) (Decapoda: Brachyura)

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Introduction

The Angular Crab, *Goneplax rhomboides* (Linnaeus) occurs in the Eastern Atlantic Ocean and Mediterranean Sea. It has been reported from the northern Irish Sea to as far south as the Cape region of South Africa (see Barnard, 1950 : 285; Ingle, 1980 : 109); the species occurs from the lower shore to depths of about 700 m.

Capart (1951 : 169) discussed regional variation of this species with respect to the degree of development of the posterior pair of carapace anterio-lateral teeth and differences in shapes of the male first pleopod. He suggested two 'varieties' may exist. Specimens attributed to *G. rhomboides* (L.) have a very rudimentary pair of posterior teeth and are reported only from the Mediterranean Sea, coast of Mauritania and the Canary Islands whereas material assigned to *G. angulata* (Pennant) has been recorded from various Atlantic Ocean localities (see Manning & Holthuis, 1981 : 164).

The larval stages of *G. rhomboides* have been described previously (see larval and post-larval references below), but these accounts are generally inadequate for use in detailed comparative studies of larval morphology. The recent rearing of *G. rhomboides* to third crab stage has provided sufficient material for redescribing the complete larval development of this species and an account is given here of the four zoeal and megalop stage.

Materials and Methods

After several unsuccessful trawling attempts, SCUBA diving was used to collect ovigerous material. On the advice of Alan Howard (MAFF) members of the BM(NH) Diving Unit searched the sandy-mud substrate to a depth of 18m off Shoalstone Point (SX937568), Brixham, Devon. An ovigerous crab was collected on 10 July 1981 and transported to the rearing laboratory of the Crustacea Section, BM(NH). The larvae were reared using methods described by Rice & Ingle (1975) and Ingle & Clark (1977), except that sea water was untreated. Drawings and measurements were made with the aid of a *camera lucida.* Measurements are as follows: total lengths of zoeae (T.T.) measured from tip of dorsal to tip of rostral spine and carapace length (C.L.) measured from between eyes to posterio-lateral margin of carapace (for zoeae) and from rostral tip for megalop. All material was fixed in Steedman's preservative (Steedman, 1976 : 148) and later transferred to 70% ethanol alcohol. The female and larval stages are deposited in the collections of the BM(NH), accession numbers 1981 : 540 & 1982 : 55 respectively.

Descriptions

Goneplax rhomboides (Linnaeus, 1758)

non *Gonoplax rhomboides:*-Cano, 1891, Tav. XI, figs 1D (or ?E), IX^{d}, IX^{e} (megalops); *Brachynotus sexdentatus:*-Cano, 1891, Tav. XI, fig. 1F (crab stage); non *Gonoplax rhomboides:*-Williamson, 1915,

Bull. Br. Mus. nat. Hist. (Zool.) **44**(2): 163–177 Issued 24 February 1983

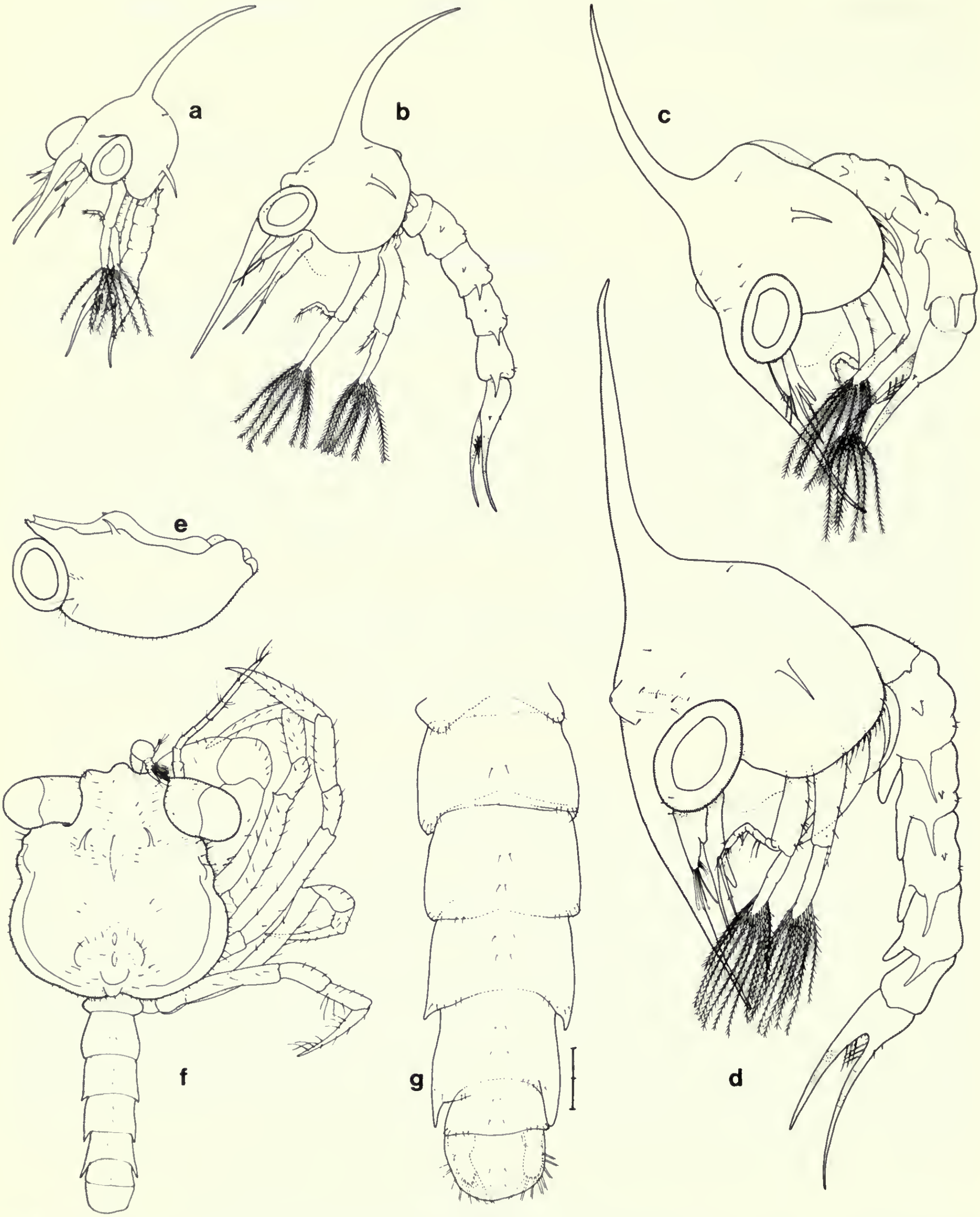

Fig. 1 *Goneplax rhomboides* (L.): a–d 1st–4th zoeae; e megalopal carapace from left lateral aspect f; megalop from dorsal aspect; g moult of megalopal abdomen slightly flattened to show setation; scale, each division = 0·1 mm.

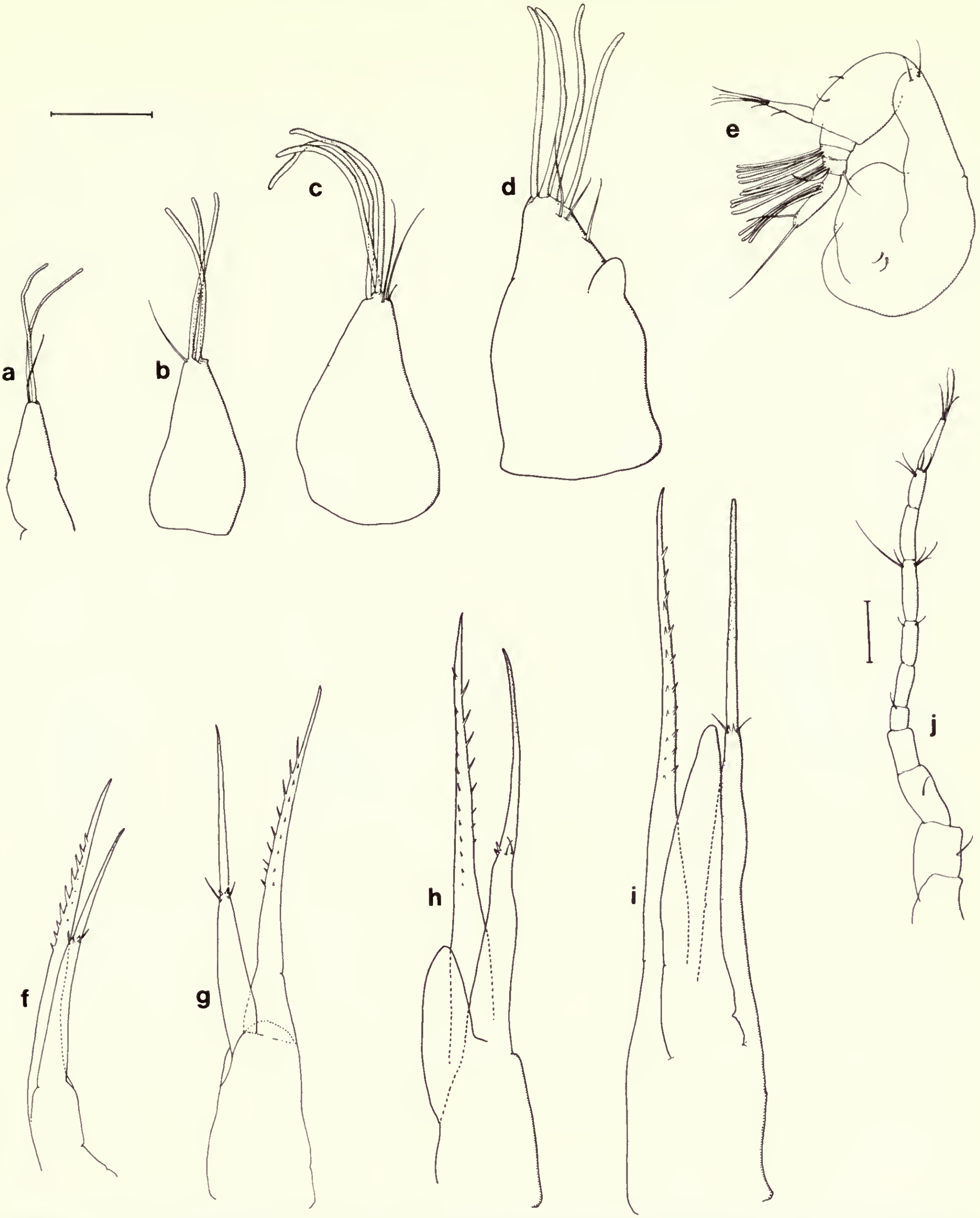

Fig. 2 *Goneplax rhomboides* (L.): a–d antennule of 1st–4th zoea respectively and e of megalop; f–i antenna of 1st–4th zoea and j of megalop respectively; scale = 0·1 mm.

fig. 398 (after Cano); *Gonoplax angulata*:- Caroli, 1927: 161 (1st–4th zoeae, megal., describ.); *Gonoplax rhomboides*:- Lebour, 1928 : 534, figs 4 (6–9), 5 (22–24), Pl. II, fig. 6, Pl. XI, fig. 10, Pl. XII, figs 1–4 (1st–4th zoeae, megal., 1st–4th crab); *Gonoplax angulata*:–Bourdillon-Casanova, 1960 : 180, figs 57a–c (1st zoea, megal.); *Goneplax rhomboides*:- Rice & Williamson, 1977 : 55, fig. 29 (3rd zoea).

FIRST ZOEA

Dimensions: T.T. 1·5 mm, C.L. 0·5 mm.

Carapace (Fig. 1a): Dorsal, rostral and lateral spines present; a pair of posterio-dorsal

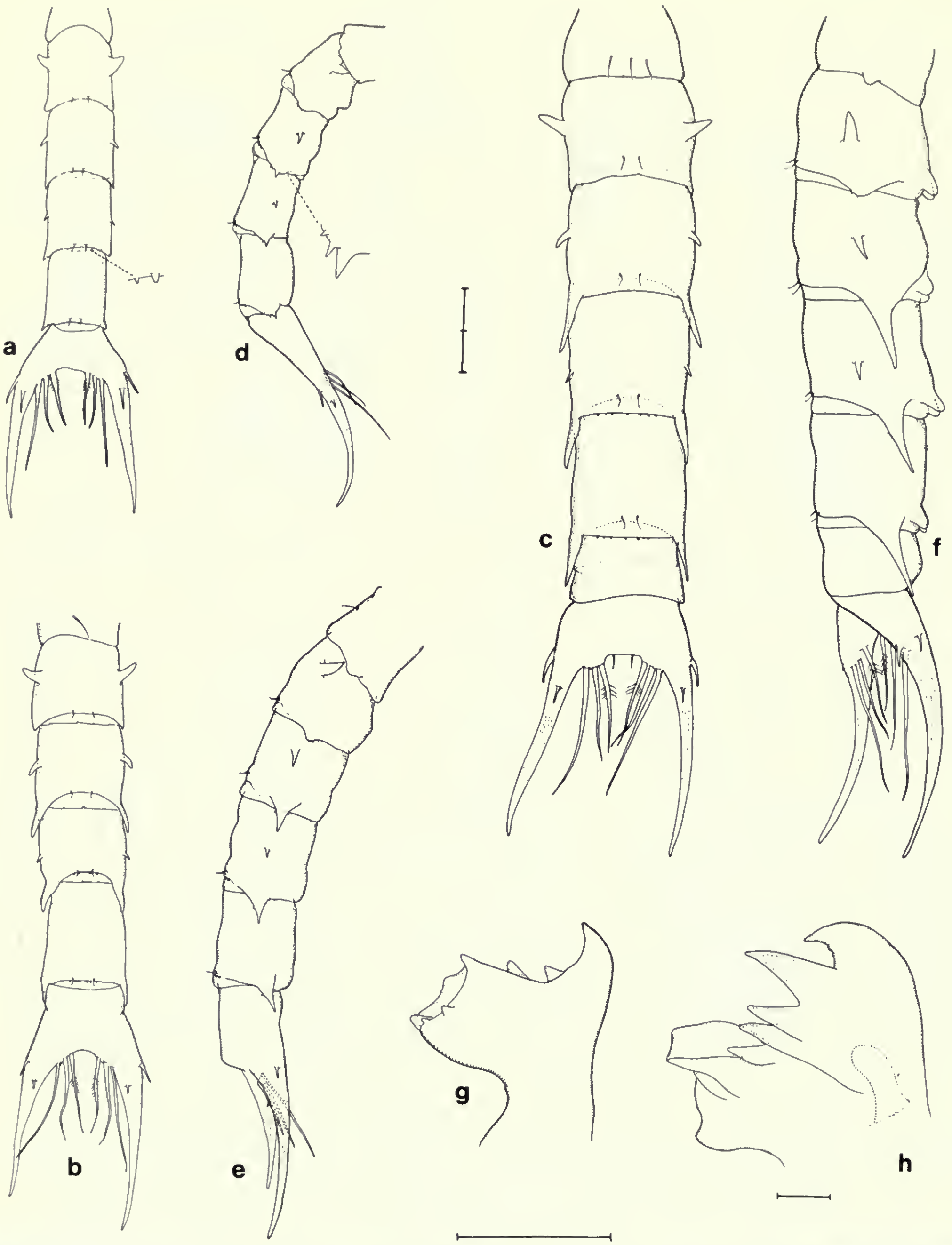

Fig. 3 *Goneplax rhomboides* (L.): a–c abdomen and telson of 1st–3rd zoea respectively from dorsal aspect and d–f same from lateral aspect; g, h left half of mandible of 1st and 4th zoea respectively (drawn from scanning EM photographs); scale, each division = 0·1 mm except h = 30μ.

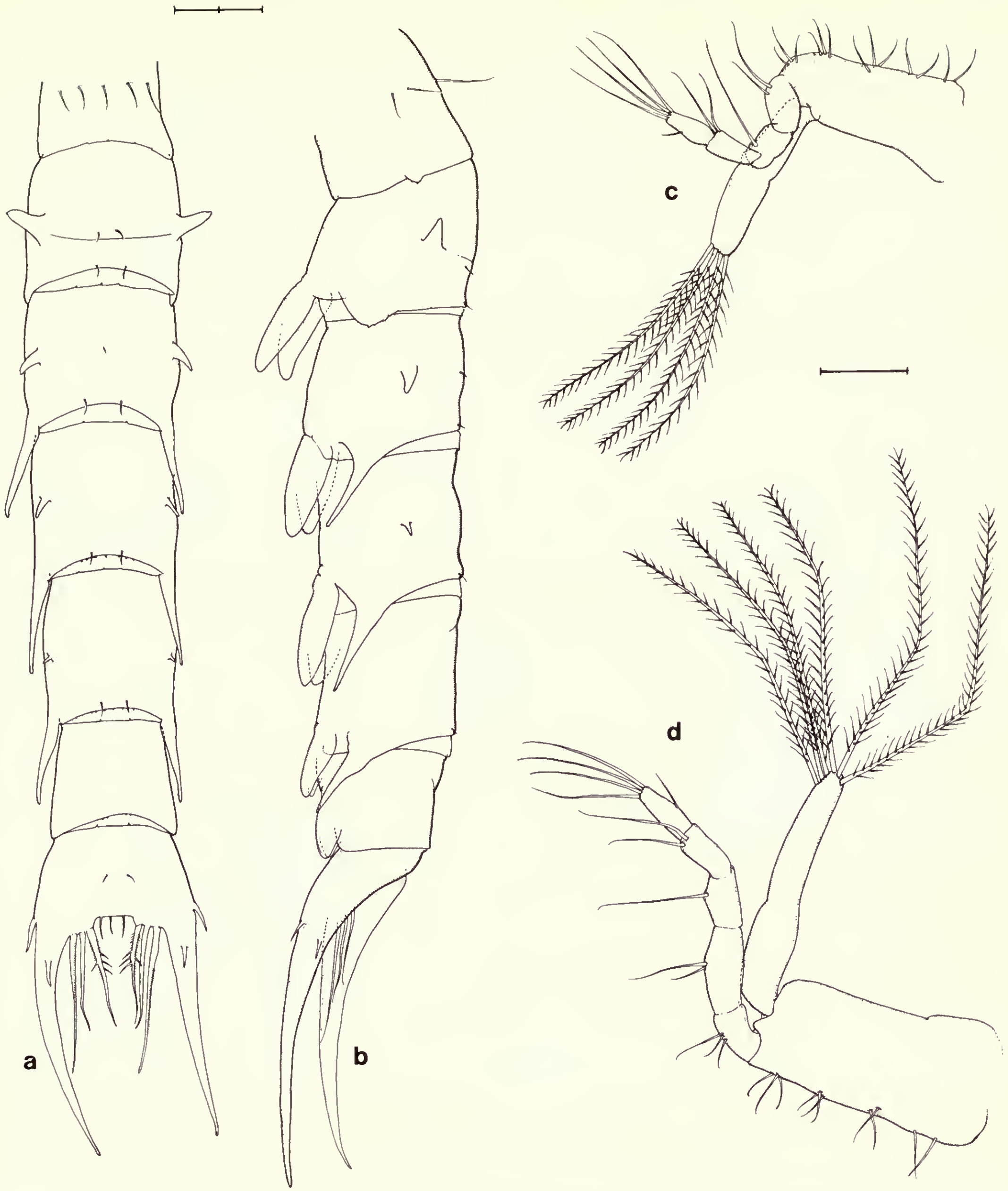

Fig. 4 *Goneplax rhomboides* (L.): a abdomen and telson of 4th zoea from dorsal aspect; b of another specimen from lateral aspect; c, d 1st maxilliped of 1st and 2nd zoea respectively; scale, each division = 0·1 mm.

setules; dorso-median elevation present; posterior margin of carapace minutely serrate and with 3–4 setules.

Eyes: Partly fused to carapace.

Antennule (Fig. 2a): Exopod unsegmented, with 2 terminal aesthetascs and one seta.

Antenna (Fig. 2f): Exopod with very minute spinules distally and with 2 median spinules and 2 setules; spinous process distally spinulate, slightly longer than exopod.

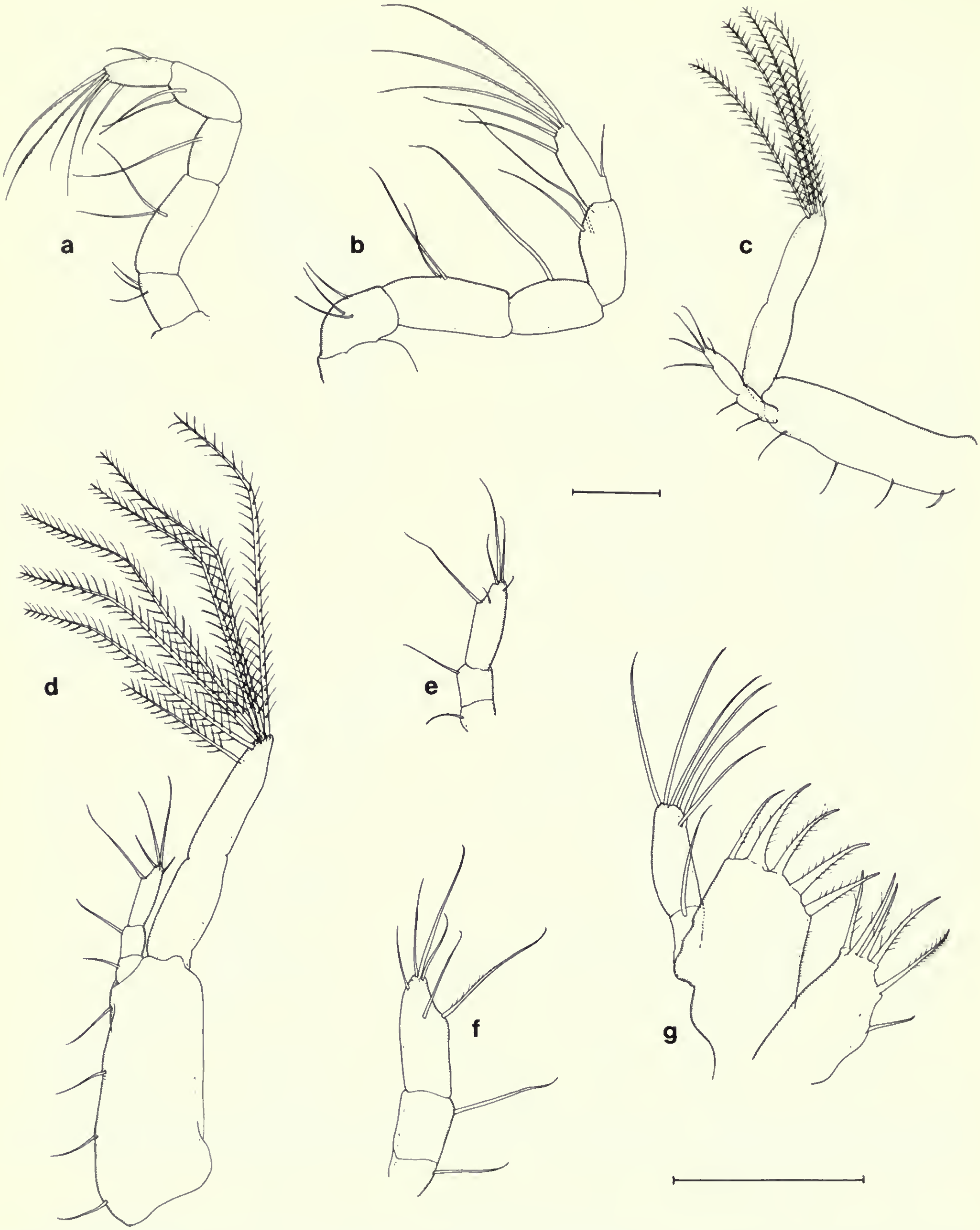

Fig. 5 *Goneplax rhomboides* (L.): a, b 1st maxilliped endopods of 3rd and 4th zoea respectively; c, d 2nd maxillipeds of 1st and 2nd zoea and e, f 2nd maxilliped endopods of 3rd and 4th zoea respectively; g maxillule of 1st zoea; scale = 0·1 mm.

Mandible (Fig. 3g): Incisor and molar processes developed.
Maxillule (Fig. 5g): Endopod 2-segmented, proximal segment with one seta, distal with 2 sub-terminal and 4 terminal setae; basal endite with one seta and 4 spines on distal margin; distal and inner margins of coxal endite with a total of 6 setae.
Maxilla (Fig. 7a): Scaphognathite with 4 long plumose setae and one distal stout posterior process; endopod bilobed, with 5+3 setae; basal endite unequally bilobed, with 4+5 setae; coxal endite bilobed with 4+4 setae.
First maxilliped (Fig. 4c): Exopod incipiently 2-segmented, with 4 terminal plumose setae; endopod 5-segmented, with 3, 2, 1, 2, 4+1 setae; margin of basis with 2, 2, 3, 3 setae.
Second maxilliped (Fig. 5c): Exopod incipiently 2-segmented, with 4 terminal plumose setae; endopod 3-segmented, with 1, 1, 4+1 setae; margin of basis with 4 setae.
Third maxilliped: not developed.
Pereiopods: not developed.
Abdomen (Figs 3a, d): 5-segmented+telson, segments 2–4 each with a pair of lateral processes decreasing in size on each respective segment; posterio-lateral margins of segments with minute denticles as shown in inset to Fig. 3d; margin of segment 2 produced and rounded, those of 3–5 with acute processes; each posterio-dorsal margin of segments 3–5 with minute denticles and of 2–5 with a pair of small setules. Telson broad, one long dorsal and one lateral spine on each fork; posterior margin concave, with 3 spines on each outer half, outermost pair longest; middle portion of telson forks invested with minute spinules.

SECOND ZOEA
Dimensions: T.T. 1·9–2·0 mm, C.L. 0·6–0·7 mm.
Carapace (Fig. 1b): Now with 2 pairs of anterio-dorsal setules, 4–6 setules on posterior margin and a prominent dorso-median elevation; eyes free.
Antennule (Fig. 2b): Exopod now with 3 terminal aesthetascs.
Antenna (Fig. 2g): Exopod setules longer than in previous stage, an incipient endopod bud present.
Mandible: Unchanged.
Maxillule (Fig. 6a): Endopod now conspicuously stepped distally; basal endite with a prominent plumose seta on outer margin, distal and inner margins with a total of 3 setae and 5 spines; distal and inner margins of coxal endite with a total of 7 setae.
Maxilla (Fig. 7b): Scaphognathite now with 12 marginal setae.
First maxilliped (Fig. 4d): Exopod now with 6 terminal plumose setae.
Second maxilliped (Fig. 5d): Exopod now with 7 terminal plumose setae.
Third maxilliped: represented as a small bud.
Pereiopods: represented as small buds.
Abdomen (Figs 3b, e): Dorsal surface of 1st segment with one seta, posterio-lateral margin now slightly produced, lateral processes on segment 2 and posterio-lateral processes on 3–5 longer than in previous stage.

THIRD ZOEA
Dimensions: T.T. 2·8–2·9 mm, C.L. 1·1–1·2 mm.
Carapace (Fig. 1c): Now with 5 pairs of anterio-dorsal setules and 7–10 setules on posterior margin.
Antennule (Fig. 2c): Exopod now with 3 setules and 3 setae.
Antenna (Fig. 2h): Endopod bud well developed.
Mandible: Incisor sub-divided.
Maxillule (Fig. 6b): Basal endite now with 3 setae on distal margin and with a total of 9 setae on distal and inner margins of coxal endite.
Maxilla (Fig. 7c): Scaphognathite now with 20 setae, basal endite with 5+5 and coxal with 4+5 setae.
First maxilliped (Fig. 5a): Exopod now with 8 terminal plumose setae; distal segment of endopod now with 5+1 setae.

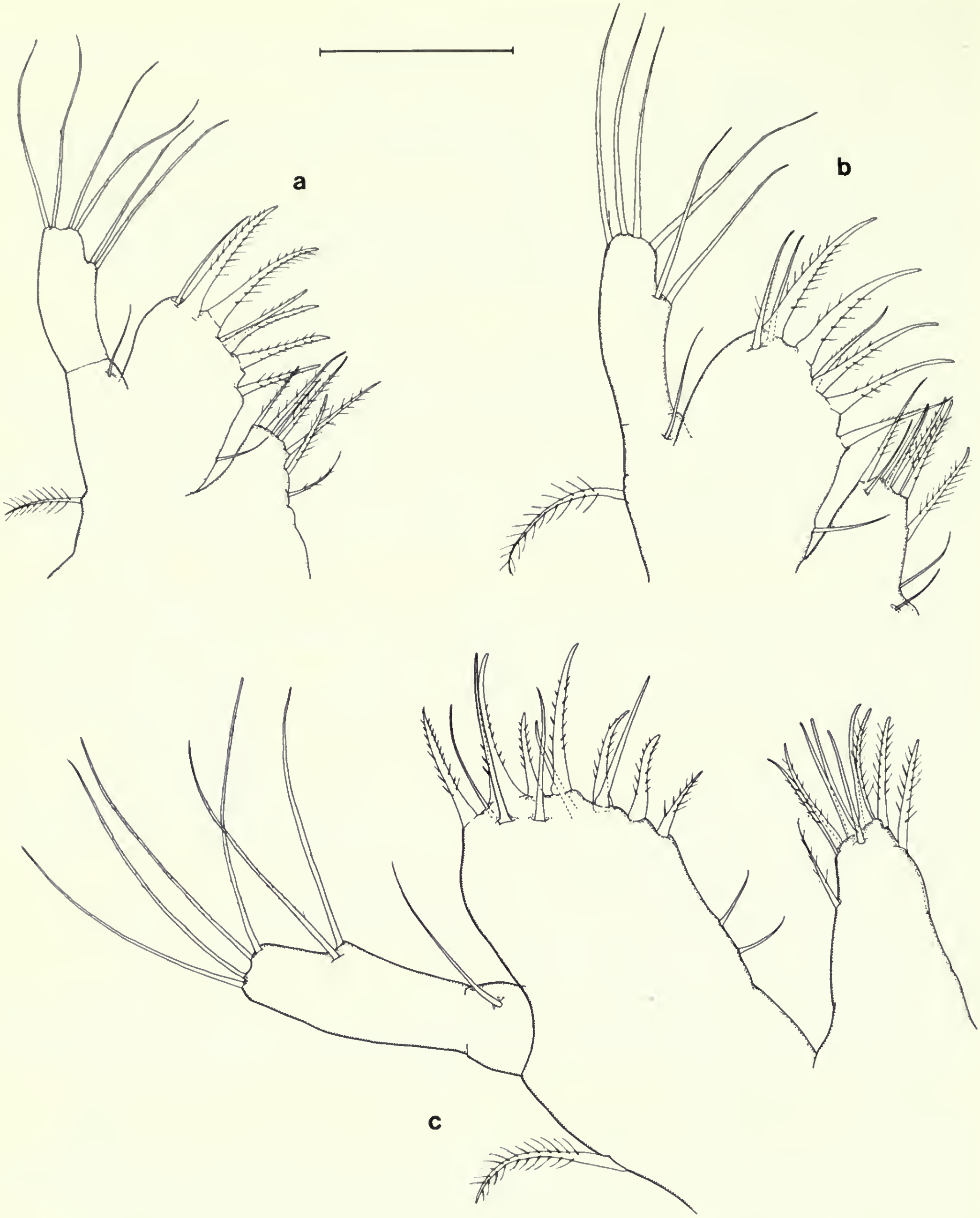

Fig. 6 *Goneplax rhomboides* (L.): a–c maxillule of 2nd–4th zoea respectively; scale = 0·1 mm.

Second maxilliped (Fig. 5e): Exopod now with 8 terminal plumose setae; distal segment of endopod with 5 + 1 setae.
Third maxilliped: represented as a conspicuous biramous bud.
Pereiopods: rudimentary but conspicuous, first pair incipiently chelate.
Abdomen (Figs 3c, f): Now 6-segmented + telson; a minute lateral process on segment 5 in some specimens; posterio-lateral processes on segments 3–5 longer than in previous stage;

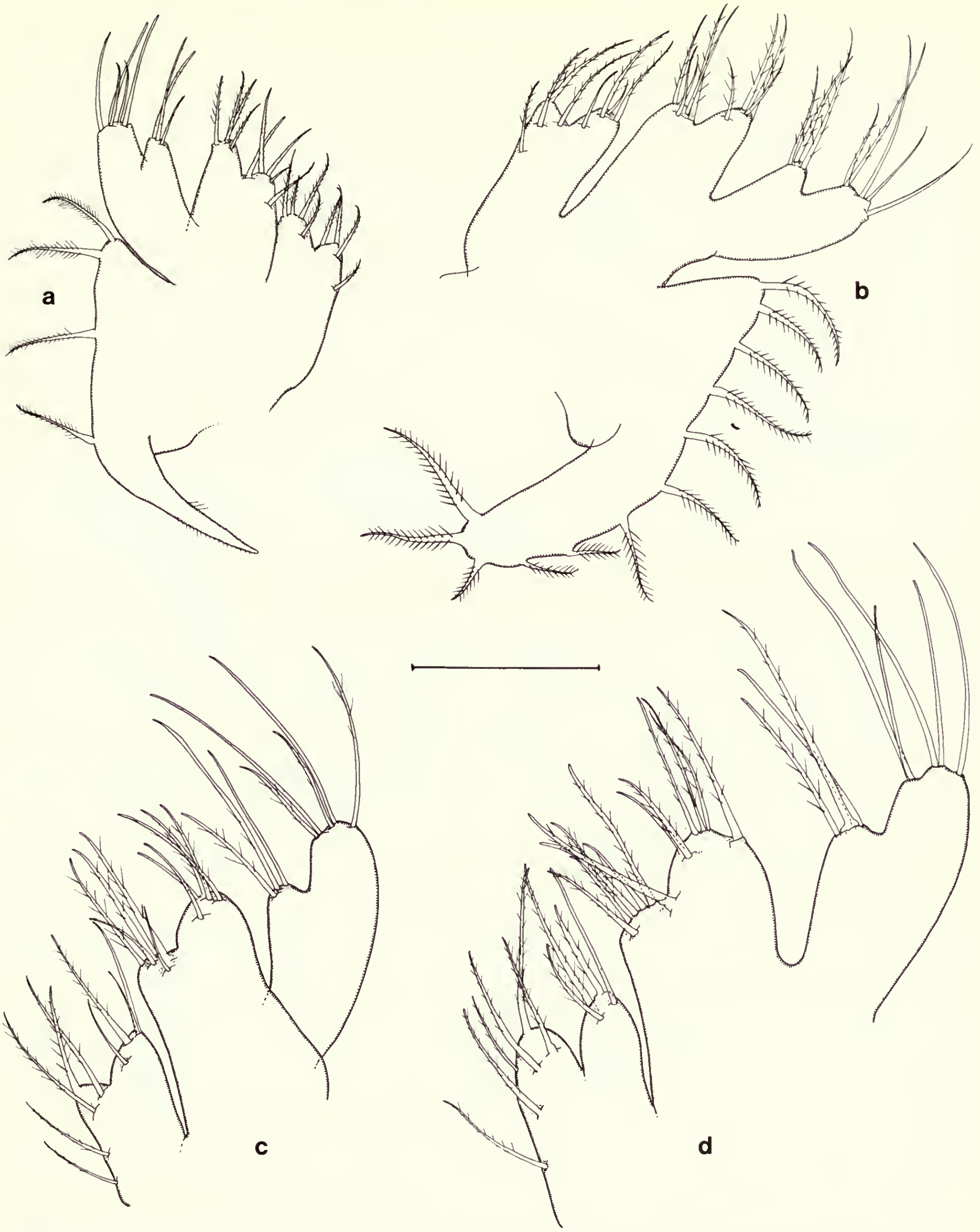

Fig. 7 *Goneplax rhomboides* (L.): a, b maxilla of 1st and 2nd zoea; c, d endopod, basal and coxal endites of maxilla of 3rd and 4th zoea respectively; scale = 0·1 mm.

dorsal surface of 1st segment now with 3 setae; rudimentary paired pleopods on segments 2–5.

FOURTH ZOEA

Dimensions: T.T. 3·5–3·6 mm, C.L. 1·4–1·5 mm.

Carapace (Fig. 1d): Now with 8 or more pairs of anterio-dorsal setules, 2 pairs at base of rostral spine and sometimes a small setule on each eye; 12–15 setules on posterior margin of carapace.

Antennule (Fig. 2d): Exopod now with 4 terminal aesthetascs and short setae; endopod represented as an incipient bud.

Antenna (Fig. 2i): Exopod now with conspicuous distal spinules; endopod bud more than half length of exopod.

Mandible (Fig. 3h): Incisor and molar processes sub-divided as shown.

Maxillule (Fig. 6c): Distal and inner margins of basal endite now with a total of 7 setae and 7 spines; margins of coxal endite with a total of 10 setae.

Maxilla (Fig. 7d): Scaphognathite now with 31 marginal setae; margins of basal endite with 6 + 6 and coxal with 4 + 6 setae respectively.

First maxilliped (Fig. 5b): Exopod now with 9 terminal plumose setae; distal segments of endopod proportionally slightly longer than in previous stage.

Second maxilliped (Fig. 5f): Exopod now with 10–11 terminal plumose setae; segments of endopod proportionally longer than in previous stage.

Third maxilliped: more conspicuous than in previous stage.

Pereiopods: more developed than in previous stage.

Abdomen (Figs 4a, b): Segment 6 now with minute denticles on posterio-dorsal margin and with a pair of pleopods; segments 1, 2, 3 with 5, 4, and 3 dorsal setae respectively; pleopods biramous. Medio-posterior margin of telson with 3 setae, dorsal surface with a pair of median setae.

MEGALOP

Dimensions: C.L. 1·8–1·9 mm.

Carapace (Figs 1e–f): Rostrum small, slightly deflected ventrally; mesogastric region with a prominent longitudinal carina; each half of protogastric region with a prominent curved spine; cardiac and intestinal regions with carinae and broad tubercles arranged as shown in Fig. 1f; margin of carapace with numerous small setules.

Antennule (Fig. 2e): Peduncle 3-segmented, with 2 setae on each segment; exopod 4-segmented with 0, 5, 4, 3 aesthetascs and 0, 0, 2, 2 setae respectively; endopod unsegmented, with one sub-terminal and 5 terminal setae.

Antenna (Fig. 2j): Peduncle 3-segmented, with 1, 1, 0 setae and flagellum 7-segmented with 1, 0, 2, 5, 0, 4, 4 setae respectively.

Mandible (Fig. 9e): Molar process now reduced, palp 3-segmented, with 0, 1, 8 setae respectively.

Maxillule (Fig. 8a): Endopod now reduced and unsegmented, with 2 terminal setae; margins of basal endite with a total of 13 setae and 8 spines; margins of coxal endite with a total of 15 setae/spines.

Maxilla (Fig. 8b): Scaphognathite with 51 marginal setae and 4 setae on dorsal surface, posterior margin sub-truncate; endopod reduced to a sub-acute lobe with setae on outer margin; basal endite with 8 + 7 marginal setae and with additional setae on dorsal and ventral surfaces as shown; coxal endite with 6 + 9–10 setae.

First maxilliped (Fig. 8c): Coxal segment with 6–7 setae, basis with 26–28 setae; endopod represented as a broad sub-acute lobe invested with 3–4 setae; exopod 2-segmented, with 3 and 5 setae respectively; epipod well developed, with 6 long setae.

Second maxilliped (Fig. 8d): Coxal segment hardly differentiated from basis, with 5–6 setae, ischium to dactylus differentiated, with 0, 3, 1, 4, 5 setae respectively in addition to 4 spines on dactylar margin; exopod 2-segmented, with 2 and 4 setae respectively; 2 setae at basis–exopod junction; epipod short, with 3 distal setae.

Third maxilliped (Fig. 9a): Coxa not differentiated from basis, with 4–5 setae as shown; outer margin of ischium with 1–2 broad, acute spines and with 19–20 setae; merus to dactylus well differentiated and with 11–12, 5, 7, 6 setae respectively; exopod 2-segmented, with 1 and 5 setae respectively; epipod long, with numerous short setae in proximal half *(circa* 18) and 15 long medio- to distally placed setae.

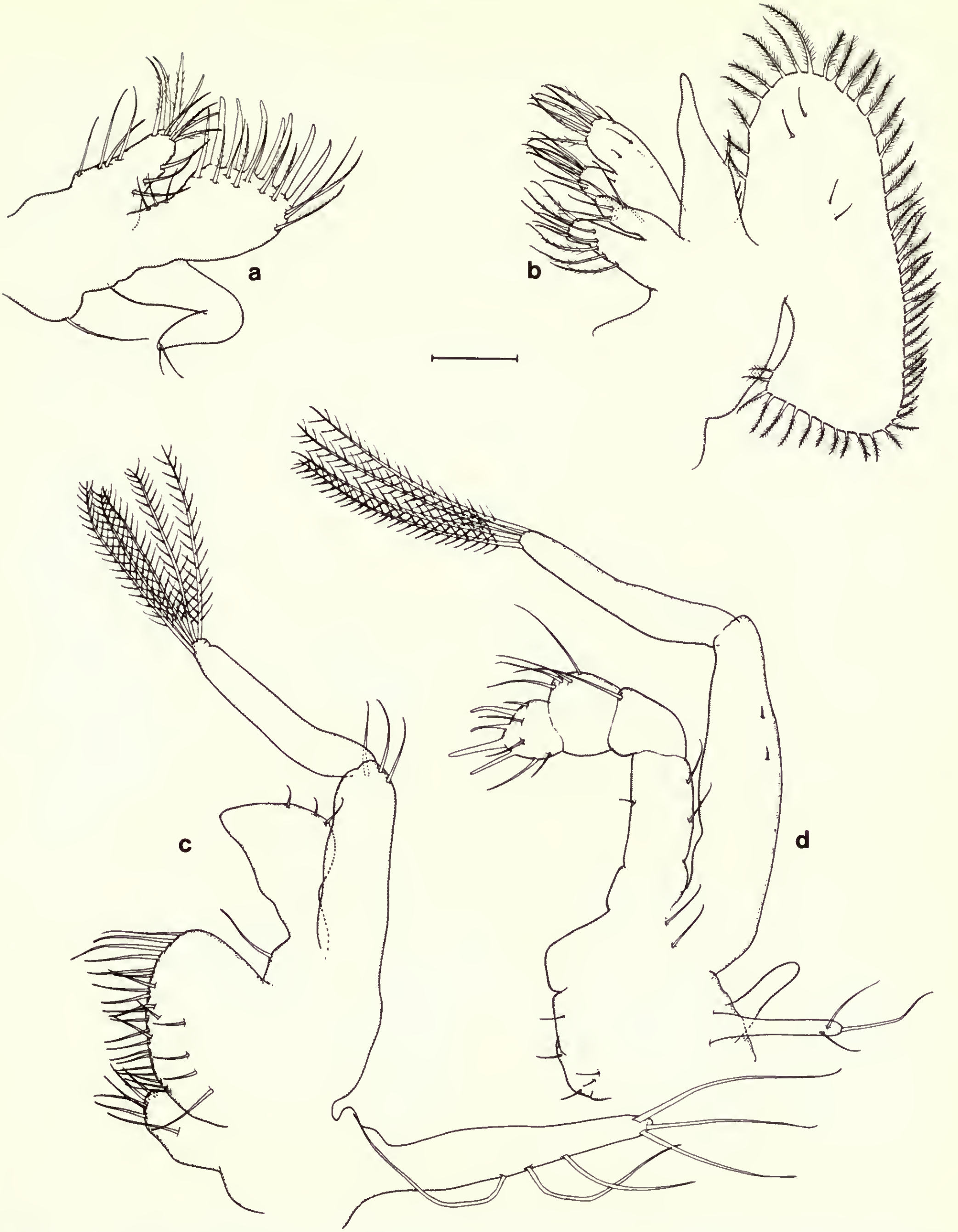

Fig. 8 *Goneplax rhomboides* (L.): megalop – a maxillule; b maxilla; c 1st maxilliped; d 2nd maxilliped; scale = 0·1 mm.

Pereiopods (Figs 9b–d, 10a, b, i): Cheliped stout, invested with numerous setae as shown in Fig. 9b; one large and one small ischial spine present; inner margin of propodal extension with 2–3 processes, inner margin of dactylus without processes. Pereiopods stout, setose as shown in Figs 9c, d & 10a, b; coxal-ischial segments of pereiopods 2–4 each with a well developed spine; dactylus of 5th pereiopod with 3 long setae on inner distal margin.

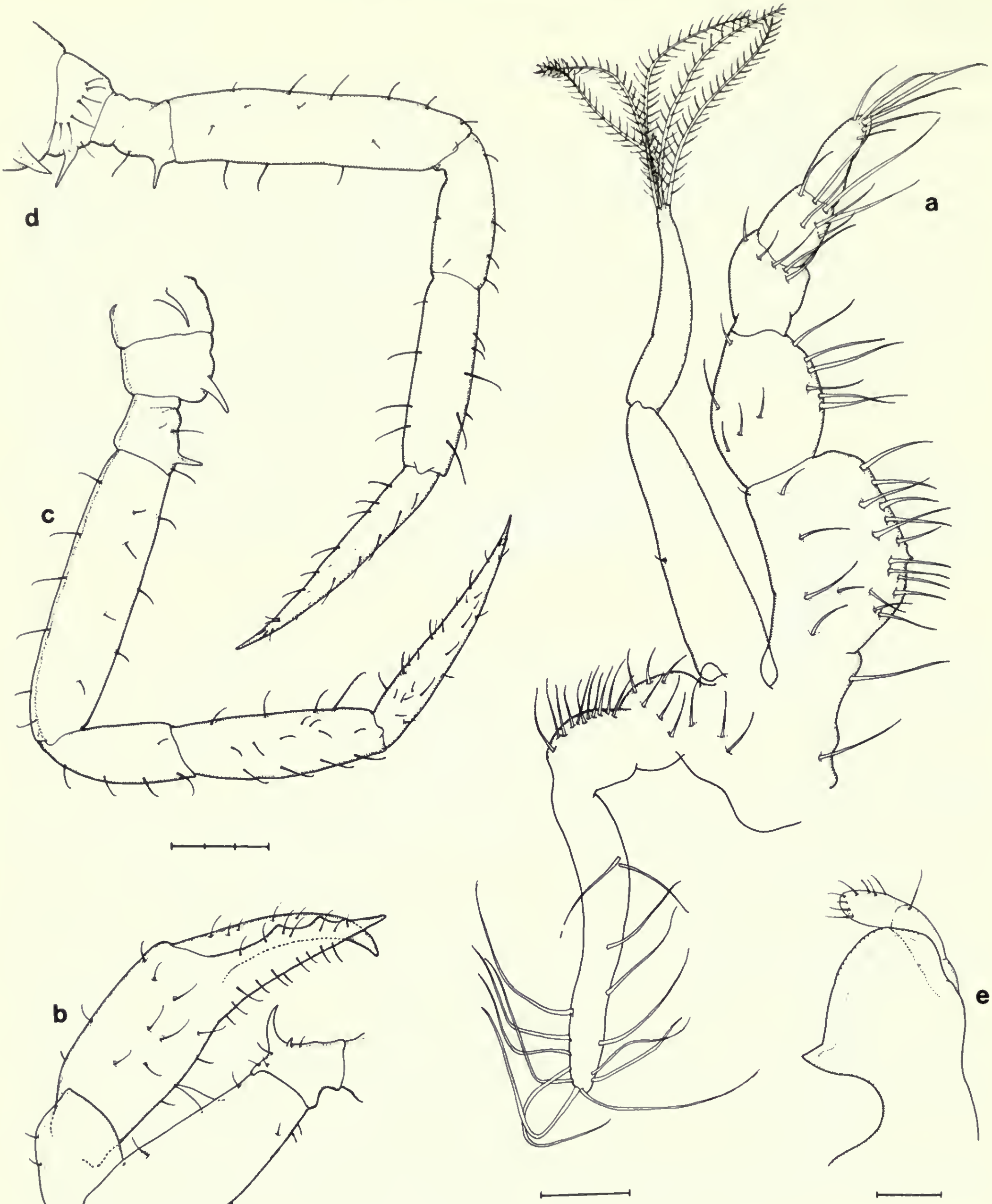

Fig. 9 *Goneplax rhomboides* (L.): megalop – a 3rd maxilliped; b left cheliped; c 2nd pereiopod; d 3rd pereiopod; e mandible; each division of scale = 0·1 mm.

Cephalothorax (Fig. 10i): Second to 4th sternites each with a prominent curved spine and a seta, first segment of sternum also with a small spine and numerous setae.

Abdomen (Figs 1f, g & 10h): 6-segmented + telson; posterio-lateral margin of first segment sub-acute, of 2nd truncate, of 3rd–5th acutely produced and of 6th sub-truncate. Surfaces of segments invested with numerous setae distributed as shown in Fig 1g. Well developed

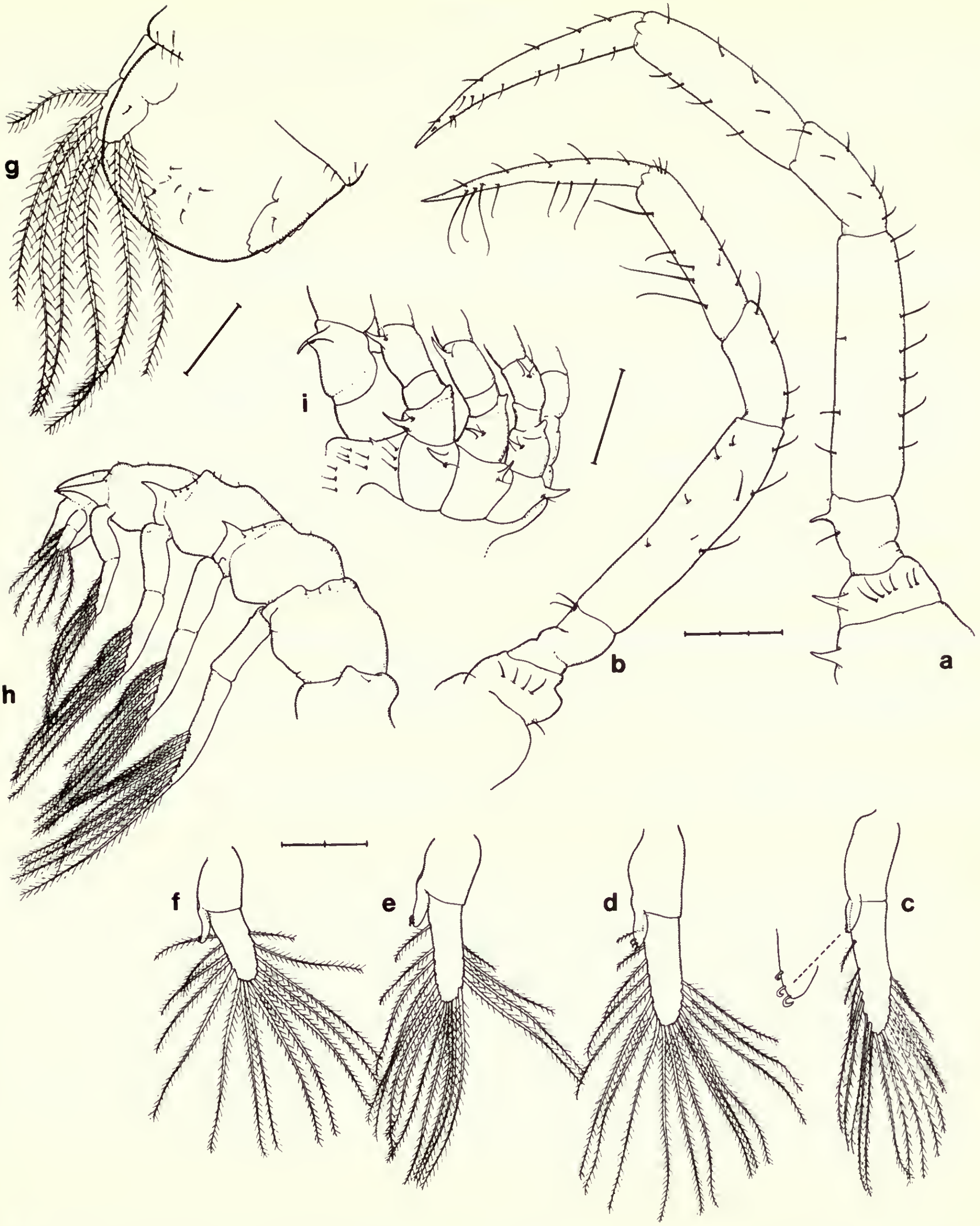

Fig. 10 *Goneplax rhomboides* (L.): megalop – a–b 4th and 5th pereiopods and c–f 1st–4th pleopods respectively; g telson and left uropod from dorsal aspect; h abdomen from right lateral aspect; i sternites and coxal-ischial segments of pereiopods from left side, ventral aspect; scale, each division = 0·1 mm.

biramous pleopods on segments 2–5, exopods with 17, 17, 16, 15 long plumose setae on 1st–4th pairs (Figs 10c–f) respectively; inner distal margin of endopod of each with 3 coupling hooks. Uropods (Fig. 10g) well developed, distal segment with 7–8 long plumose setae. Telson much broader than long, dorsal surface with a pair of lateral and 2 pairs of median setules, ventral surface with 3–4 small setules.

Remarks

The present laboratory reared material of *G. rhomboides* differs in a number of features from the accounts given by Bourdillon-Casanova (1960) and Rice & Williamson (1977). These differences are tabulated below.

Bourdillon-Casanova	**Present material**
ZOEA I	ZOEA I
Denticles on proximal part of posterio-lateral margin of abdominal segments very pronounced.	Denticles on proximal part of posterio-lateral margin of abdominal segments very minute.
MEGALOP	MEGALOP
Disto-lateral margins of rostrum very acute.	Disto-lateral margins of rostrum not acute.
Protogastric spines of carapace stout and straight.	Protogastric spines of carapace thin and curved.
A pair of widely spaced tubercles on metabranchial-intestinal regions.	A pair of tubercles placed near to median line on cardiac region.
Groups of setae on posterior region of carapace	Without groups of setae on posterior region of carapace.
Exopod of uropod with 8–9 setae	Exopod of uropod with 7–8 setae.
Rice & Williamson	
ZOEA III	ZOEA III
Antennal exopod with a single mid-point seta.	Antennal exopod with more than one seta/spinule at mid-point.
Scaphognathite of maxilla with 18–19 setae.	Scaphognathite of maxilla with 20 setae.
Endopod of 2nd maxilliped with 1, 1, 5 setae.	Endopod of 2nd maxilliped with 1, 1, 6 setae.
ZOEAE 1–IV	ZOEAE I–IV
Exopod terminal segment of 2nd maxilliped with 4, 7, 9, 11 setae in respective stages.	Exopod terminal segment of 2nd maxilliped with 4, 7, 8, 10–11 setae in respective stages.

With the exception of *Geryon tridens* (Kröyer), the zoeae of *Goneplax rhomboides* can be distinguished from those of other known brachyrhynchs occurring in the N.E. Atlantic sea area (see Ingle, 1980) by the following combined features: (1) A pair of small but prominent dorso-lateral processes on the 4th segment of the abdomen and sometimes a minute pair on the 5th segment in the 3rd and 4th stages. (2) The antennal exopod with spinules and setae sub-terminally placed. Features separating zoeae of *G. rhomboides* from those of *Geryon tridens* were tabulated by Ingle (1979 : 229). The following amendments must now be made to this table with respect to *G. rhomboides*: (1) The antennal exopod–the spinous process is longer than the exopod in all stages. (2) Maxilla of ZIII-scaphognathite with a maximum of 20 setae on margin. (3) 1st maxilliped-endopod setae of ZIII, *G. tridens* 2, 2, 1, 2, 5 + 1 and *G. rhomboides* 3, 2, 1, 2, 5 + 1 respectively.

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The larval and first crab stages of three *Inachus* species (Crustacea: Decapoda: Majidae); a morphological and statistical analysis

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Introduction

Several authors have acknowledged difficulties in distinguishing between congeneric brachyuran crab·larvae (see Lebour, 1928 : 546; Hartnoll, 1961 : 181; Christiansen, 1969; Rice & Ingle, 1975*a* & 1975*b*; Ingle, 1982). These observations were based on a limited amount of material that did not permit statistical analysis of larval characters. Rearing large numbers of crab larvae (see Ingle & Clark, 1977) provided sufficient material for this statistical study. A multivariate technique was used to examine the larvae and first crab stage of three species of spider crabs belonging to the genus *Inachus*.

Material & Methods

Berried females of *Inachus dorsettensis* and *I. phalangium* were collected by trawl from localities off Port Erin, Isle of Man, and Plymouth and *I. leptochirus* was trawled from *Modiolus* beds four miles south of Spanish Head, Isle of Man. The adult females, together with the larvae used in this study are deposited in the BM(NH). Larvae were reared using methods described by Ingle & Clark (1977), then fixed and preserved in 80% alcohol. Twenty specimens of each stage were dissected and mounted as permanent slide preparations in lignin pink/polyvinyl lactophenol. For the multivariate study 43, 142 & 178 characters were used for zoeal, megalop and first crab stages respectively. The majority of these characters are meristic, e.g. setal counts on appendages, but a few were present or absent scores. Accurate measurements of spines and carapace dimensions, as well as carapace setal counts of megalops and crab stages proved to be impracticable and were not used. Setal counts were scored for one side of the body although on occasions it was necessary to combine parts of both left and right appendages to form a complete score. The data was subjected to Principal co-ordinate analysis according to Gower (1966). This method summarizes similarities between OTUs as a 2-dimensional plot. The computation was carried out using a varian V 72 computer. Each larval stage was analysed separately to avoid major differences between stages swamping any specific variation.

Results

Statistical Analysis

First and second principal co-ordinates were plotted for zoea II, megalops and first crab stage of each species. The zoea I stage data was not computed because only two characters were considered significant on inspection. The OTUs in zoea II (Fig. 1) can be separated into two groups, *I. leptochirus* and *I. dorsettensis/I. phalangium* whereas in both megalops (Fig. 2) and first crab stage (Fig. 3) they are clearly separated into three groups which correspond to the three species.

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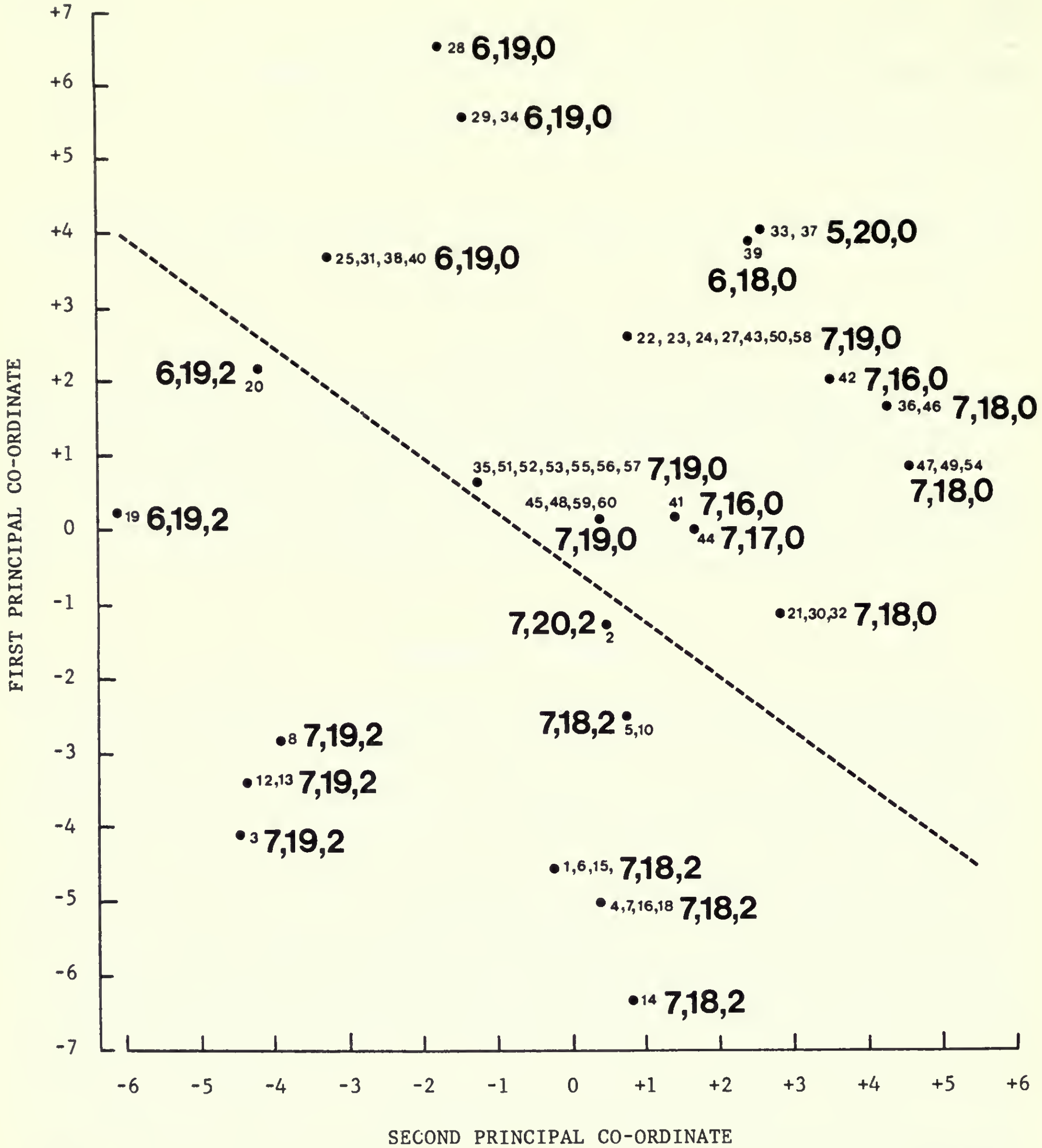

Fig. 1 A plot of the 1st & 2nd Principal co-ordinates of zoea II. Scores of variate 1 (range **5, 6, 7**), variate 11 (range **16, 17, 18, 19, 20**) and variate 36 (range **0, 2**) are plotted against their OTUs. OTUs 1–20 *I. leptochirus*, 21–40 *I. dorsettensis*, 41–60 *I. phalangium*. The dotted line divides the OTUs into two groups, group 1 = *I. leptochirus* and group 2 = *I. dorsettensis/I. phalangium.* Variate 36 is the only diagnostic character separating the two groups. Note that the dotted line has no statistical significance.

The zoea I stages can be divided into two groups, *I. leptochirus* and *I. dorsettensis/I. phalangium,* using the basal article of the second maxilliped and the posterio-dorsal margin of the first abdominal somite. *I. leptochirus* has one seta on the basis (Fig. 4b) and two on the first abdominal somite (Fig. 4c) whereas *I. dorsettensis* and *I. phalangium* have no setae at either site (Fig. 4a, d). The first zoeal stages of *I. dorsettensis* and *I. phalangium* cannot be separated on setal characters.

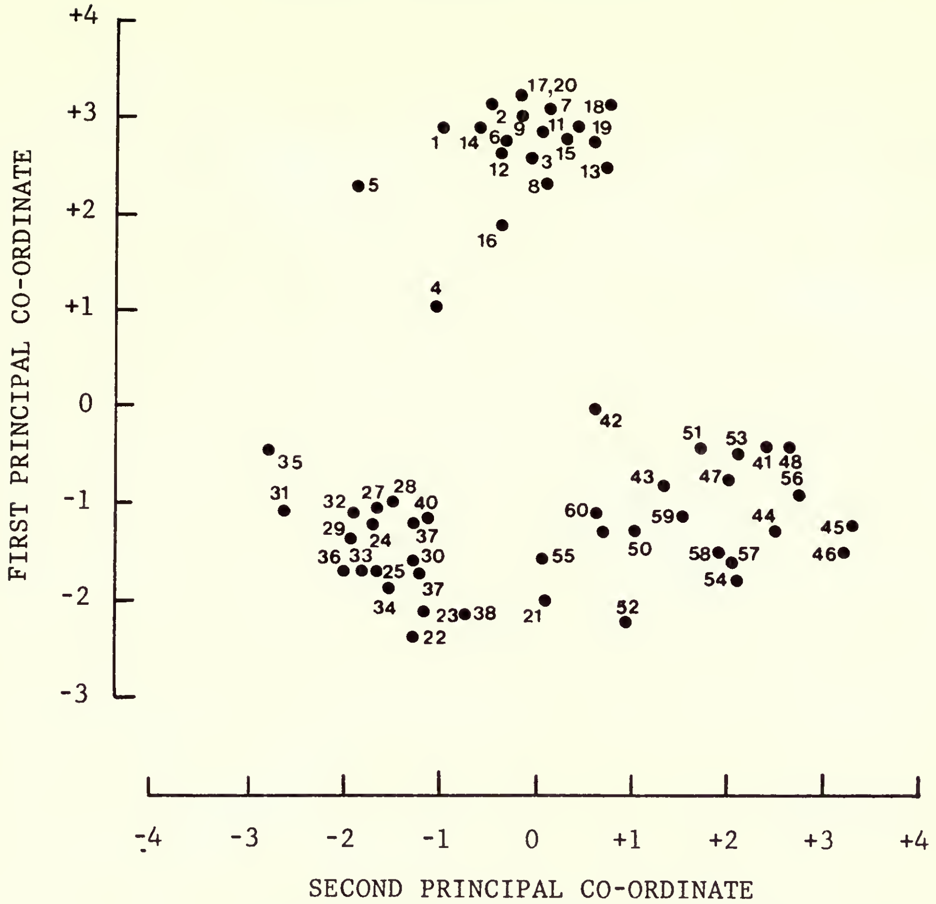

Fig. 2 A plot of the 1st & 2nd Principal co-ordinates of megalops using 68 variates. OTUs 1–20 *I. leptochirus,* 21–40 *I. dorsettensis,* 41–60 *I. phalangium.* These OTUs fall into 3 distinct groups which correspond to the three British *Inachus* species.

The second zoeal stages can also be split into the same two groups (Fig. 1). The three characters showing variation were the number of terminal aesthetascs on the antennule, the numbers of setae on the margin of the maxillary endopod and on the posterio-dorsal margin of the first abdominal somite. The scores of these three characters are shown respectively on Fig. 1 in bold type, adjacent to their respective OTUs. Separation of the two groups shown by the dotted line is determined only by one character, the number of posterio-dorsal marginal setae on the first abdominal somite. *I. leptochirus* has 2 setae (Fig. 4c) whereas *I. dorsettensis* and *I. phalangium* have none (Fig. 4d).

The megalops can be divided into three groups which correspond to the three species using only 68 out of the original 142 characters (Fig. 2). Group separation remains constant however, if only nine characters are used.

By using combinations of the means of these nine characters it seems possible to separate the megalops of the three species.

Nevertheless, their overlapping distribution (Table 2) makes separation very difficult in practice as no single character separates all three species. For example, OTU 21 *(I. dorsettensis)* is grouped with OTUs 52 and 53 *(I. phalangium)* on its overall similarity as they have identical scores for all nine characters. Overlapping ranges of variation in numbers of setae makes it impossible to differentiate all three species with absolute confidence at the

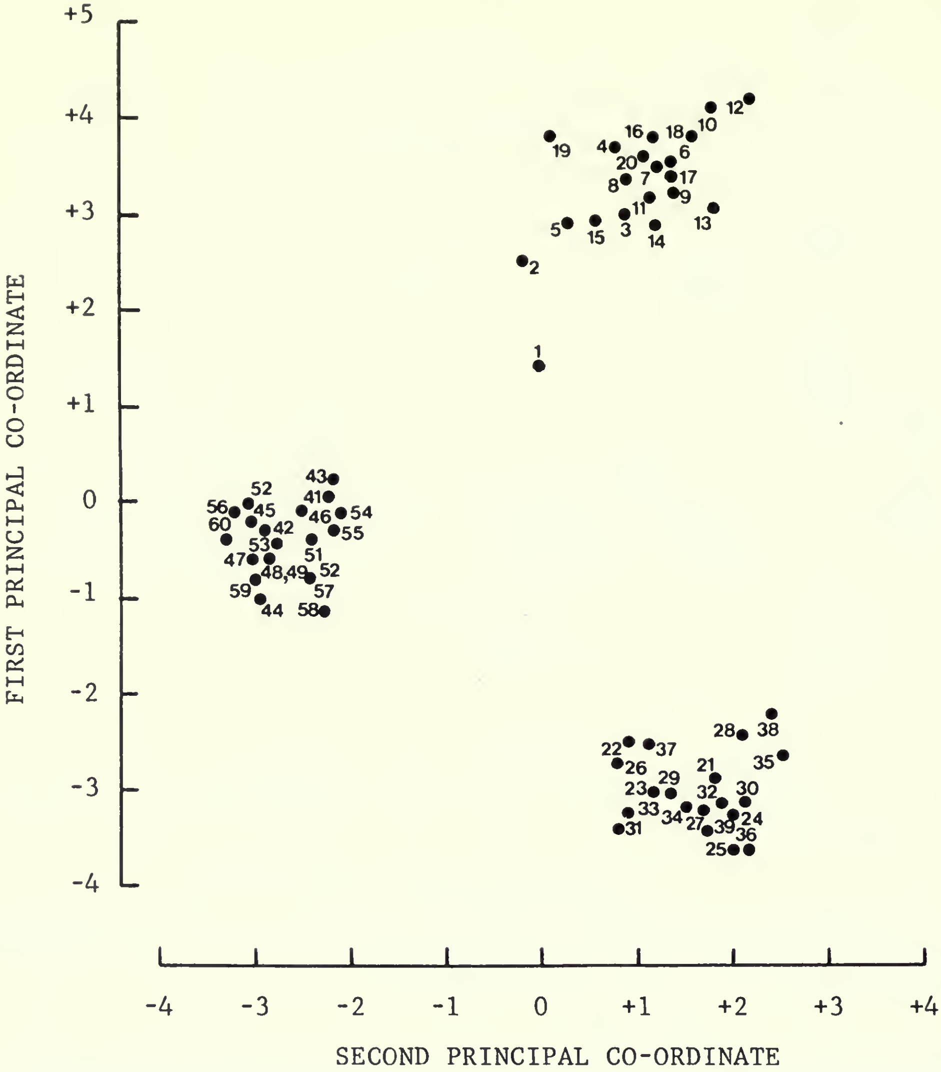

Fig. 3 A plot of the 1st & 2nd Principal co-ordinates of the first crab stages using 138 variates. OTUs 1–20 *I. leptochirus*, 21–40 *I. dorsettensis*, 41–60 *I. phalangium*. These OTUs fall into 3 distinct groups which correspond to the three British *Inachus* species.

megalop stage. Only the number of setae on the proximal exopod segment of the antennule (Figs. 4e, f) displays no intraspecific variability and serves as a diagnostic character separating *I. leptochirus* from *I. dorsettensis/I. phalangium.* The number of spines on the merus of the first peraeopd is also a relatively good character separating *I. leptochirus* from the other two species, but this is a particularly difficult character to observe because of the thickness of the merus.

Differentiation of the first crab stage OTUs (Fig. 3) was achieved using 138 characters from the original 178, but clustering of the OTUs corresponding to the three *Inachus* species does not alter when the number of characters is reduced to 21 (Fig. 5). These 21 characters are listed in Table 3.

As with the megalops, separation of the three species is marked when the means of the variates (Table 4) are used, but again the distributions show considerable overlap. In

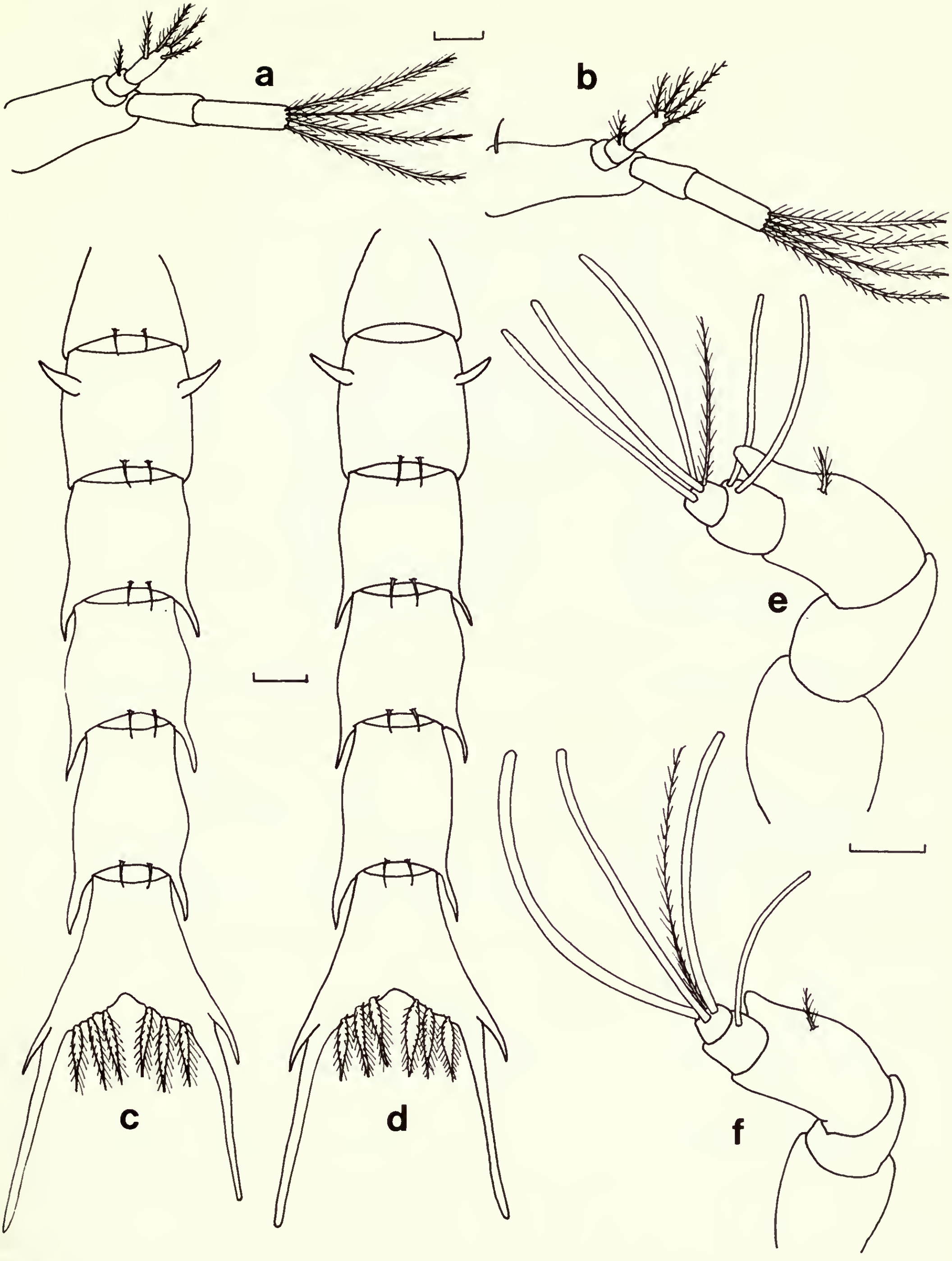

Fig. 4 2nd maxilliped, zoea I (a) *I. dorsettensis* & *I. phalangium* (b) *I. leptochirus*; abdomen of zoea I & II (c) *I. leptochirus* (d) *I. dorsettensis* & *I. phalangium*; antennule of megalop (e) *I. leptochirus* (f) *I. dorsettensis* & *I. phalangium.*

Table 1 A list of characters that may separate the megalops of the three *Inachus* species

Variate no.	Characters
4	number of setae on proximal exopod segment of antennule
7	number of setae on first segment of antenna
44	number of setae on merus of 3rd maxilliped
48	number of setae on epipodite of 3rd maxilliped
62	number of spines on merus of 1st peraeopod
67	number of setae on propodus of 2nd peraeopod
81	number of setae on propodus of 3rd peraeopod
95	number of setae on propodus of 4th peraeopod
109	number of setae on propodus of 5th peraeopod

Table 2 Studying the means of each character from Table 1, the megalops in theory are separable using combinations of characters. However, if the distribution of each character is tabulated only variate 4 is a good diagnostic character, but this only separates *I. leptochirus* from *I. dorsettensis/I. phalangium* (see Figs. 4e, f). (L = *I. leptochirus*, D = *I. dorsettensis* & P = *I. phalangium*)

distribution of variate 4

	1	2	mean
L	0	20	2
D	20	0	1
P	20	0	1

variate 4 separates L from D & P

distribution of variate 7

	0	1	mean
L	0	20	1
D	2	18	1
P	15	5	0

variate 7 separates P from D & L

distribution of variate 44

	4	5	mean
L	1	19	5
D	18	2	4
P	16	4	4

variate 44 separates L from D & P

distribution of variate 48

	0	1	2		mean
L	0	0	7	13	3
D	1	9	8	2	2
P	0	5	10	5	2

variate 48 separates L from D & P

distribution of variate 62

	2	3	4	mean
L	0	0	20	4
D	0	20	0	3
P	4	15	1	3

variate 62 separates L from D & P

distribution of variate 67

	16	17	18	mean
L	3	17	0	17
D	19	1	0	16
P	0	19	1	17

variate 67 separates D from L & P

distribution of variate 81

	15	16	17	mean
L	0	2	18	17
D	1	19	0	16
P	0	3	17	17

Variate 81 separates D from L & P

distribution of variate 95

	15	16	17	mean
L	0	6	14	17
D	4	16	0	16
P	1	10	9	16

variate 95 separates L from D & P

distribution of variate 109

	14	15	16	mean
L	1	2	17	16
D	0	20	0	15
P	1	18	1	15

variate 109 separates L from D & P

Note that the means have been rounded up to the nearest whole number.

Table 3 List of characters that may be used to separate the 1st crab stages

Variate no.	Characters
6	aesthetascs on 2nd exopod segment of antennule
9	setae on endopod of antennule
13	number of setae on 3rd segment of antenna
14	number of spines on 1st segment of antenna
21	number of setae on distal segment of mandibular palp
45	number of setae on basis of 2nd maxilliped
57	number of setae on coxa of 3rd maxilliped
94	number of setae on basis of 2nd peraeopod
99	number of spines on merus of 2nd peraeopod
100	number of spines on ischium of 2nd peraeopod
114	number of setae on ischium of 3rd peraeopod
115	number of setae on basis of 3rd peraeopod
120	number of spines on merus of 3rd peraeopod
121	number of spines on ischium of 3rd peraeopod
135	number of setae on ischium of 4th peraeopod
136	number of setae on basis of 4th peraeopod
141	number of spines on merus of 4th peraeopod
146	number of hooks on propodus of 4th peraeopod
156	number of setae on ischium of 5th peraeopod
157	number of setae on basis of 5th peraeopod
167	number of hooks on propodus of 5th peraeopod

practice, only a combination of characters can be used to distinguish between the species at first crab stage.

Morphology

The general morphology of *I. dorsettensis* was described and illustrated by Ingle (1977). Most of the setal counts fall within the variation recorded during the present study. This indicates little or no temporal variation. Some of the discrepancies may be due to the difficulty of classifying and objectively defining elements, as between a seta and a spine, when the structures grade one into the other (Gurney, 1931 : 38). However, some disparity between Ingle's study and the present work could not be accounted for.

Discussion

Williamson (1965 : 390) listed the presence of a seta on the outer margin of the maxillule basal endite as one of ten characters for separating brachyuran larvae from anomuran larvae. In previous descriptions of zoea II in majids this character is shown as present, for example, Ingle (1977) records this seta as present in zoae II and megalops of *Inachus* reared from Plymouth material — this was confirmed by re-examining Ingle's material and by rearing fresh material from the Plymouth area. In this study the seta was absent from zoea II of *I. dorsettensis* reared from the Isle of Man and from all three megalops.

Lebour* (1928) suggested that larvae of the three *Inachus* species could be separated on size, chromatophore patterns and length of dorsal spines, but none of these claims could be verified. Only the megalops and first crab stage of *I. leptochirus* in the present study proved to be larger than those of the other two species. Larval inachinids have apomorphic zoeal characters which were listed by Rice (1980 : 307), to which can now be added the absence of

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*Lebour's material is no longer extant; Ingle, pers. comm.

Table 4 Studying the means of each character from Table 3, the first crab stages may be using a combination of characters. However, if the distribution of each character is tabulated it is evident that no one character is completely diagnostic. (L=*I. leptochirus,* D= *I. dorsettensis* & P=*I. phalangium)*

distribution of variate 6

	1	2	3	mean
L	0	2	18	3
D	18	2	0	1
P	20	0	0	1

variate 6 separates L from P & D

distribution of variate 9

	3	4	mean
L	1	19	4
D	17	3	3
P	18	2	3

variate 9 separates L from P & D

distribution of variate 13

	2	3	4	mean
L	0	19	1	3
D	20	0	0	2
P	0	14	6	3

variate 13 separates D from P & L

distribution of variate 18

	2	3	4	mean
L	0	2	18	4
D	2	9	9	3
P	1	13	6	3

variate 18 separates L from P & D

distribution of variate 21

	0	1	2	mean
L	0	0	20	2
D	0	14	6	1
P	1	19	0	1

variate 21 separates L from P & D

distribution of variate 45

	0	1	mean
L	0	20	1
D	12	8	0
P	17	3	0

variate 45 separates L from P & D

distribution of variate 57

	4	5	6	7	8	9	10	11	mean
L	1	0	0	3	6	4	5	1	8
D	0	5	15	0	0	0	0	0	6
P	0	3	17	0	0	0	0	0	6

variate 57 separates L from P & D

distribution of variate 94

	0	1	2	mean
L	0	2	18	2
D	1	19	0	1
P	0	1	19	2

variate 94 separates D from P & L

distribution of variate 99

	0	1	mean
L	3	17	1
D	19	1	0
P	20	0	0

variate 99 separates L from P & D

distribution of variate 100

	0	1	2	mean
L	0	0	20	2
D	15	4	1	0
P	3	8	8	1

variate 100 separates L from P & D

distribution of variate 114

	3	4	5	6	mean
L	0	1	18	1	5
D	1	18	1	0	4
P	0	0	19	1	5

variate 114 separates D from L & P

distribution of variate 115

	1	2	mean
L	1	19	2
D	20	0	1
P	0	20	2

variate 115 separates D from L & P

distribution of variate 120

	0	1	mean
L	2	18	1
D	19	1	0
P	20	0	0

variate 120 separates L from P & D

distribution of variate 121

	0	1	2	mean
L	1	3	16	2
D	6	12	2	1
P	2	17	1	1

variate 121 separates L from P & D

distribution of variate 135

	4	5	6	mean
L	1	16	3	5
D	20	0	0	4
P	1	17	2	5

variate 135 separates D from P & L

distribution of variate 136

	1	2	3	mean
L	1	19	0	2
D	20	0	0	1
P	3	16	1	2

variate 136 separates D from P & L

distribution of variate 141

	0	1	mean
L	3	17	1
D	18	2	0
P	20	0	0

variate 141 separates L from D & P

distribution of variate 146

	2	3	4	5	mean
L	1	16	3	0	3
D	20	0	0	0	2
P	0	18	1	1	3

variate 146 separates D from L & P

distribution of variate 156

	1	5	6	mean
L	0	17	3	5
D	19	1	0	4
P	1	17	2	5

variate 156 separates D from L & P

distribution of variate 157

	0	1	2	mean
L	0	0	20	2
D	1	19	0	1
P	0	0	20	2

variate 157 separates D from P & L

distribution of variate 167

	2	3	mean
L	0	20	3
D	20	0	2
P	3	17	2

variate 167 separates D from P & L

Note that the means have been rounded up to the nearest whole number.

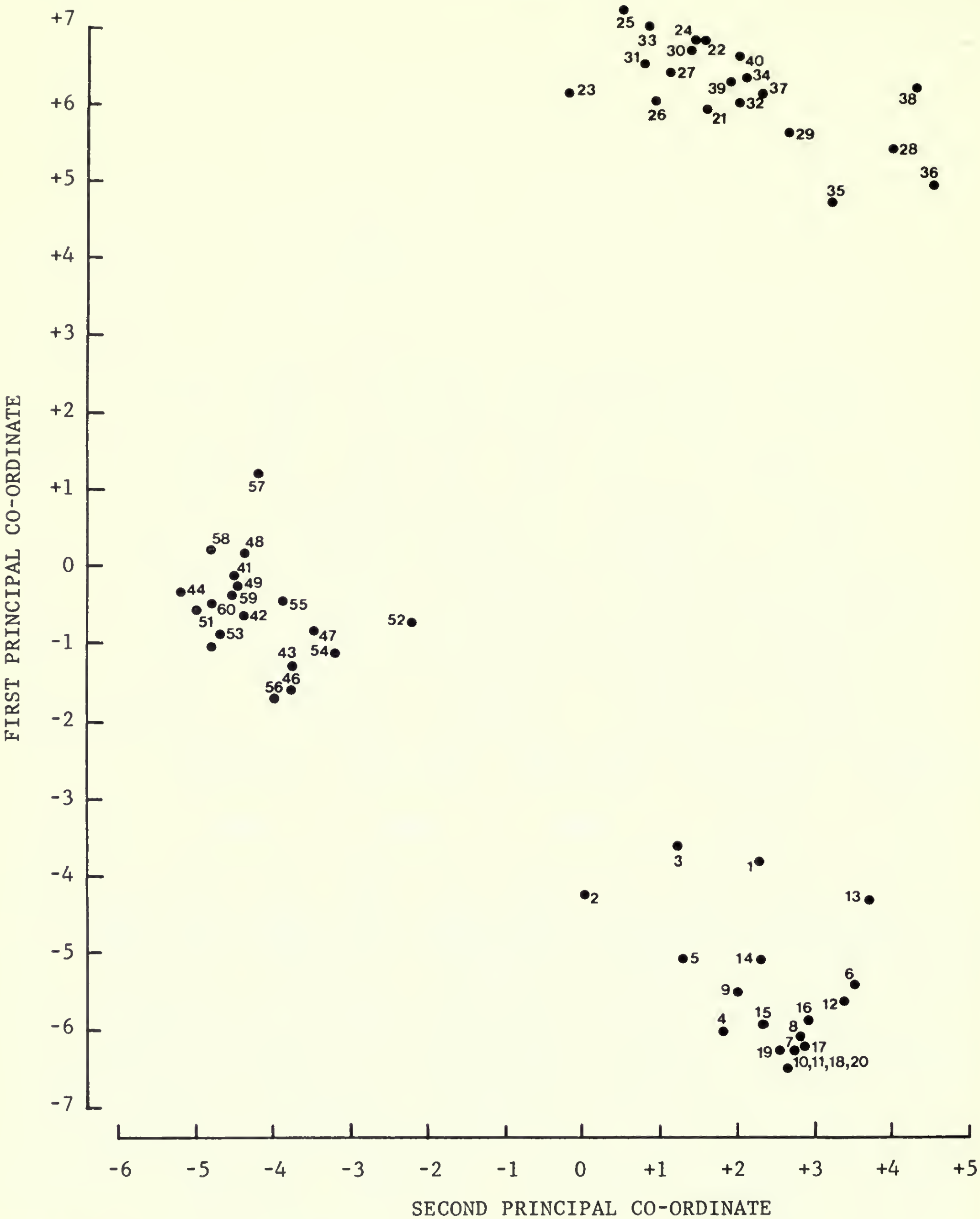

Fig. 5 A plot of the 1st and 2nd Principal co-ordinates of first crab stage using 21 variates. OTUs 1–20 *I. leptochirus*, 21–40 *I. dorsettensis*, 41–60 *I. phalangium*. Although the number of variates is reduced from 138 to 21, the OTUs still fall into 3 distinct groups which correspond to the 3 British *Inachus* species. The grouping of the OTUs is similar to that in Fig. 3 and therefore illustrates that the 21 characters selected contribute to the separation of the 3 groups. Note that the groups *I. leptochirus* and *I. dorsettensis* have changed positions when compared with Fig 3; this has no significance in the analysis.

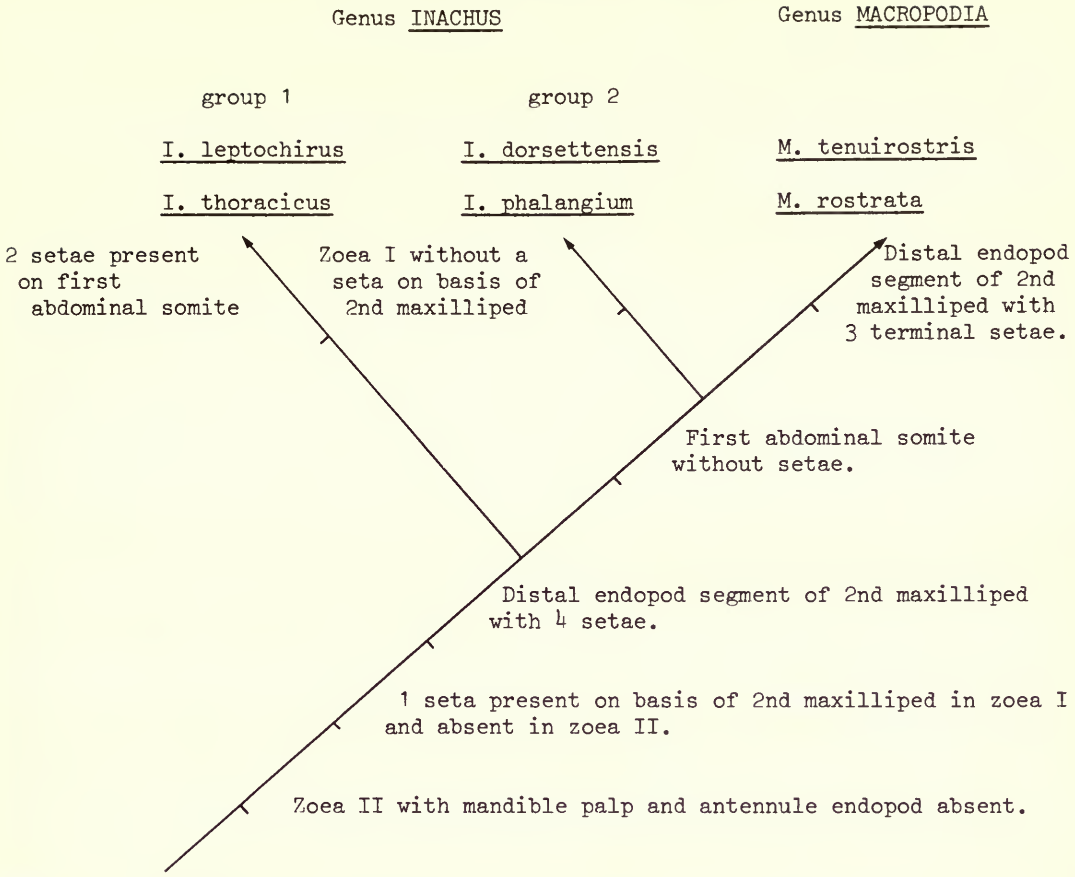
Genus INACHUS
Genus MACROPODIA
group 1
group 2
I. leptochirus
I. thoracicus
I. dorsettensis
I. phalangium
M. tenuirostris
M. rostrata
2 setae present on first abdominal somite
Zoea I without a seta on basis of 2nd maxilliped
Distal endopod segment of 2nd maxilliped with 3 terminal setae.
First abdominal somite without setae.
Distal endopod segment of 2nd maxilliped with 4 setae.
1 seta present on basis of 2nd maxilliped in zoea I and absent in zoea II.
Zoea II with mandible palp and antennule endopod absent.

Fig. 6 Cladogram of known *Inachus* & *Macropodia* larval descriptions.

a mandibular palp and endopod bud on the antennule of zoea II. Similarly, when compared with other majid larva characters the loss of paired dorsal setae on the first abdominal somite and the absence of setae on the basis of the 2nd maxilliped in *I. dorsettensis* and *I. phalangium,* can be considered as derived traits. The present study failed to reveal characters which separate the larvae of *I. dorsettensis* from *I. phalangium,* but demonstrated that the larvae of *I. leptochirus* can be easily recognized.

Adult males of *I. leptochirus* share one important feature with two other species of *Inachus* (i.e. *I. thoracicus* & *I. aquiarii)* in having a sternal callosity, a character that is absent in males of *I. dorsettensis, I. phalangium* and *I. communissimus.* Such a separation of *Inachus* species into two groups, those with and those without a sternal callosity, is supported by the present study. Heegaard (1963) studied the zoeae of *I. thoracicus* and clearly figures two setae on the first abdominal somite (p. 475, Fig. 83), but not a seta on the basis of the 2nd maxilliped (p. 475, Fig. 82). Unfortunately Heegaard's material is no longer extant. Re-examination of *I. thoracicus* zoeae may well show that they are inseparable from *I. leptochirus,* adding support to the suggestion that there are two natural groups in the genus *Inachus.*

Present larval evidence supports the view that *Inachus* and *Macropodia* are the most derived of all majids since they show the greatest reduction in numbers of setae; considered by Rice (1980) to be the derived condition. A suggested phylogeny of well documented larvae from the genera *Inachus* and *Macropodia* is shown in Fig. 6.

Setal studies of other brachyuran genera have shown that the larvae of species accepted as closely related are not usually separable on quantitative characters. Therefore meristic setal incongruities within genera, as shown here for *Inachus*, may be the only morphological evidence of phylogenetic non-homogeniety.

This project formed part of an M.Sc. degree in Modern Taxonomy. All relevant data and larval figures were deposited in the Crustacea Section, BM(NH) and the Library of the Polytechnic of Central London.

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Amphipods are both numerous and diverse in numbers of genera and species in British coastal waters, but in the absence of any form of modern systematic synopsis or key this group of crustaceans has acquired the reputation of being notoriously difficult to identify. This monograph, which is the first comprehensive and illustrated text on British gammaridean amphipods to be published in more than a century, should go a long way towards solving the problem.

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The work has been carefully edited to bring corresponding descriptions, keys and figures into close proximity within the text. The systematic section is supported by chapters dealing with morphology, systematics, geographical distribution, biology and ecology, the latter being presented in the form of an annotated subject index of research literature. Finally, there is an extensive bibliography of about 1,200 references that includes most of the British marine amphipod literature published to date.

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Colin R. Curds & Irene C. H. Wu

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A review of the Euplotidae (Hypotrichida, Ciliophora)

Colin R. Curds & Irene C. H. Wu

Zoology Department, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Introduction

Guides to the species of two genera of Euplotid ciliates, *Euplotes* Ehrenberg *in* Hemprich and Ehrenberg, 1831 and *Aspidisca* Ehrenberg, 1830, have been published in recent years (Curds, 1975; Wu & Curds, 1979). The other genera in the family Euplotidae Ehrenberg, 1838 contain fewer species but there are still identification problems in some. The present work is intended to aid the specific identification of the remaining nine genera which Borror (1972) grouped together into the Euplotidae, another more recently described genus and one other addition. Although four of these genera only contain single species it was thought worthwhile to include them for completeness. The genera included here are in chronological order of authority. *Discocephalus* Ehrenberg *in* Hemprich and Ehrenberg, 1828; *Diophrys* Dujardin, 1841; *Uronychia* Stein, 1859; *Certesia* Fabre-Domergue, 1885; *Gastrocirrhus* Lepsi, 1928; *Euplotaspis* Chatton and Séguéla, 1936; *Euplotidium* Noland, 1937; *Paraeuplotes* Wichterman, 1942; *Swedmarkia* Dragesco, 1954; *Gruberella* Corliss, 1960 and *Cyatharoides* Tuffrau, 1975.

Members of the Euplotidae are hypotrichs with the characteristically prominent adoral zone of membranelles (AZM) arranged at the anterior left of the ventral surface bordering a wide peristome. In certain genera the AZM may continue over the apical end of the body onto the dorsal surface. Unfortunately there is no set of characters which will include all of Borror's (1972) genera into the family. This could well indicate that it is not a natural family. The cirri on the ventral surface are arranged in distinct groups but they are not the only hypotrichs to have this feature. For example, the Oxytrichidae Ehrenberg, 1838 also have grouped cirri, and Borror (1972) distinguished them from the Euplotidae by their possession of only a few left marginal and no right marginal cirri, even so there are several exceptions to

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this rule. Furthermore, while right caudal cirri are present in *Diophrys*, *Discocephalus*, *Euplotes* and *Uronychia*, they are absent in others. However, transverse cirri are present in all but one Euplotid genus. With this state of affairs, perhaps it is not surprising that there is some disagreement in the literature as to what constitutes the family Euplotidae. Borror (1972) included Aspidisca in the family but Stein (1859*a*), Bütschli (1889), Kahl (1932), Fauré-Fremiet (1961) and Corliss (1961, 1977, 1979) all maintain it in a separate family the Aspidiscidae Ehrenberg, 1838. Corliss (1979) included four genera in the family Aspidiscidae; *Aspidisca*, *Euplotaspis*, *Onychaspis* Stein, 1859 and *Paraeuplotes* (as an *incertae sedis*). The genus *Onychaspis* differs from *Aspidisca* only by the former's possession of a larger number of transverse cirri and most authors consider it to be a synonym of *Aspidisca* (Borror, 1972; Wu and Curds, 1979). Indeed, Corliss (1979) indicated this possibility in his classification. One of the features of the Aspidiscidae is the great reduction of oral membranelles, however this description would not fit the AZM of *Euplotaspis* or *Paraeuplotes*. Corliss (1979) also placed three of the genera being considered here (*Cirrhogaster* Ozaki and Yagui, 1941; *Euplotidium* and *Gastrocirrhus*) into the family Gastrocirrhidae Fauré-Fremiet, 1961. Here the single species genus *Cirrhogaster* is regarded as a member of the genus *Gastrocirrhus* as it only differs slightly in cirral number. Borror (1972) included *Gastrocirrhus* in the Euplotidae but noted that its position in that family was provisional.

It is clear from this brief synopsis that the position of these genera within three or a single family group is still in a state of flux and to a large extent a matter of conjecture. It is not the purpose of the present paper to attempt to assign the genera to any old, current or new classification scheme; more data, particularly concerning their comparative morphogenesis, are required before anything useful can be suggested. The aim here is to aid the marine ecologist and protozoologist to identify the species of those genera which conveniently fall within the single family Euplotidae.

Key to Genera

1	AZM conspicuous, in single anterior part	2
	AZM inconspicuous, in 2 parts	***ASPIDISCA*** (see Wu & Curds, 1979)
2	Without frontoventral cirri, caudals never extremely large	***GRUBERELLA*** (p. 242)
	With frontoventral cirri (when frontoventrals reduced and inconspicuous then caudals usually very large)	3
3	With caudal cirri	4
	Without caudal cirri	11
4	With marginal cirri, caudals sometimes very large	5
	Without marginals, caudals present but never very large	7
5	Caudals very large and prominent	6
	Caudals weak	***EUPLOTES*** (see Curds, 1975)
6	5 – 10 conspicuous frontoventral cirri present, moves forwards	***DIOPHRYS*** (p. 197)
	3 inconspicuous cirri present, moves backwards	***URONYCHIA*** (p. 215)
7	Elongate with discoid 'head' region	***DISCOCEPHALUS*** (p. 193)
	Ovoid to elongate, when elongate never with discoid 'head' region	8
8	Ovoid, dorsoventrally flattened	9
	Elongate, rounded in section, often cup-shaped with funnel-shaped peristome opening apically and ventrally	10
9	Cirri mainly in 2 rows, found on coral	***PARAEUPLOTES*** (p. 239)
	Cirri in well-defined groups, found in sea-squirts	***EUPLOTASPIS*** (p. 232)
10	With 5–6 transverse cirri	***EUPLOTIDIUM*** (p. 234)
	Without transverse cirri	***GASTROCIRRHUS*** (p. 228)
11	Without marginal cirri, rounded in section	***EUPLOTIDIUM*** (p. 234)
	With marginal cirri, dorsoventrally flattened	12
12	Marginal cirri on both right and left sides, confluent posteriorly	***SWEDMARKIA*** (p. 240)
	Marginal cirri on either right or left sides	13
13	Marginal cirri on left, not planktonic	***CERTESIA*** (p. 227)
	Marginal cirri on right, planktonic	***CYATHAROIDES*** (p. 243)

Genus *DISCOCEPHALUS* Ehrenberg, 1828

Introduction

The genus *Discocephalus* was erected by Ehrenberg *in* Hemprich and Ehrenberg (1828) and although his description and illustration of the type species *D. rotatorius* were crude, it was clear that the organism had a distinctive discoid 'head' formed by a constriction at the anterior end of the elongate oval body. Bütschli (1889) expressed some doubt concerning the observations of Ehrenberg (1831) but it was not until Kahl (1932), that *Discocephalus* was adequately described. The latter description concerned an organism which Kahl (1932) considered to be *D. rotatorius* Ehrenberg and of which he thought *Polycoccon octangularis* Sauerbrey, 1928 to be a junior synonym. Later, however, Dragesco (1960) isolated an organism from Roscoff which although identical to that described by Kahl (1932) was different in several respects from *D. rotatorius* Ehrenberg. Dragesco (1960) therefore named the species found at Roscoff *D. ehrenbergi* and designated *D. rotatorius* Kahl to be its junior synonym. However, Dragesco (1960) agreed that *Polycoccon octangularis* Sauerbrey was a synonym of *D. rotatorius* Ehrenberg. In addition to the two species mentioned above two others, *D. grandis* Dragesco, 1954 and *D. minimus* Dragesco, 1968, have been described.

There is a well developed AZM in all four of the above species which borders the small ventral peristome on the left of the discoid 'head'. In one species, *D. ehrenbergi*, there are 5–7 large membranelle-like structures lying along the right border of the peristome which Dragesco (1968) called 'pre-membranelles'. This character enables the diagnosis and separation of *D. ehrenbergi* Dragesco from *D. rotatorius* Ehrenberg which lacks these 'membranelles'.

The cirral patterns on the ventral surface of *Discocephalus* differ greatly from those of *Euplotes* and as their morphogenesis is yet to be published fully it is difficult to interpret them adequately. Furthermore as the cirri vary considerably from species to species, it is possible that *Discocephalus* is really a polyphyletic group. The present confusion in different terms used for the same cirri by different authors can be illustrated by reference to 'marginal' cirri. In *D. rotatorius* and *D. ehrenbergi* there are two 'marginal' cirri on the left body edge just below the peristome. However, in *D. grandis*, Dragesco (1954) refers to the presence of three rows of 'marginal' cirri which is more characteristic of members of the Oxytrichidae rather than the Euplotidae. Furthermore, in *D. minimus* there is one row of cirri on the right body edge called ventral cirri and one row on the left edge called 'marginal' cirri. Until further morphogenetic information becomes available the present authors prefer to follow in part the system used by Hartwig and Parker (1977) which distinguishes left, central and right ventral cirri rather than to attempt to distinguish marginal from ventral rows simply on the basis of their position on the ventral surface. However, it is preferable to call the most posterior cirri, left and right caudal cirri, rather than left and right posterior 'marginals' as used in Hartwig and Parker (1977). The dorsal surface of *Discocephalus* has received less attention than that of either *Euplotes* (Curds, 1975) or *Aspidisca* (Wu & Curds, 1979) but both Dragesco (1965) and Kahl (1932) have illustrated *D. ehrenbergi* with six kineties on the dorsal surface. Dorsal argyrome patterns as found in *Euplotes* and *Aspidisca* (Curds, 1975: Wu & Curds, 1979) have yet to be described. This means that the four species must currently be distinguished on the basis of their size, numbers and distribution of cirri, the presence or absence of membrane-like structures on the right of the peristome and the nature of the macronuclear apparatus. Corliss (1979) described this as a curious genus which he included only 'tentatively' in the Euplotidae and indeed, the unique body shape, the cirral arrangement and large number of macronuclear parts may well be considered sufficient for placing it in a separate family.

Diagnosis of *Discocephalus*

Oval marine hypotrichs with an anterior constriction of the body which forms a discoid 'head' containing the peristome and AZM on the left. Ventrally there are 4–8 frontal, 5–11 transverse (including satellites) and variable numbers and arrangements of ventral cirri. Posterio-dorsally there are 3–4 right caudal and 9–30 left caudal cirri. The size varies between 50–200 µm long and there are numerous macronuclei.

Key to the species of *Discocephalus*

1	With 2 left ventral cirri	2
	With 7 to many left ventral cirri	3
2	With 5 transverse cirri but without 'pre-membranelles'	***D. rotatorius***
	With 8–9 transverse cirri and several 'pre-membranelles'	***D. ehrenbergi***
3	Large (200 µm), row of many (about 40) left ventral cirri	***D. grandis***
	Small (50 µm), row of few (7–8) left ventral cirri	***D. minimus***

Species descriptions

Discocephalus rotatorius Ehrenberg, 1828 *in* Hemprich and Ehrenberg

Polycoccon octangulus Sauerbrey, 1928

DESCRIPTION (Fig. 1). Medium sized (70–100 µm long) marine species whose elongate, oval body is typically discocephalic. There is a well developed AZM bordering the left of the peristome area. The 7–8 frontal cirri are restricted to the anterior 'head' region. The ventral cirri are in two groups: there are 2–4 on the right body edge and 2 on the left immediately behind the peristome. There are 5 prominent transverse cirri. The caudal cirri are also in two groups and arise dorso-laterally: on the right are 3–4 large prominent caudals and on the left

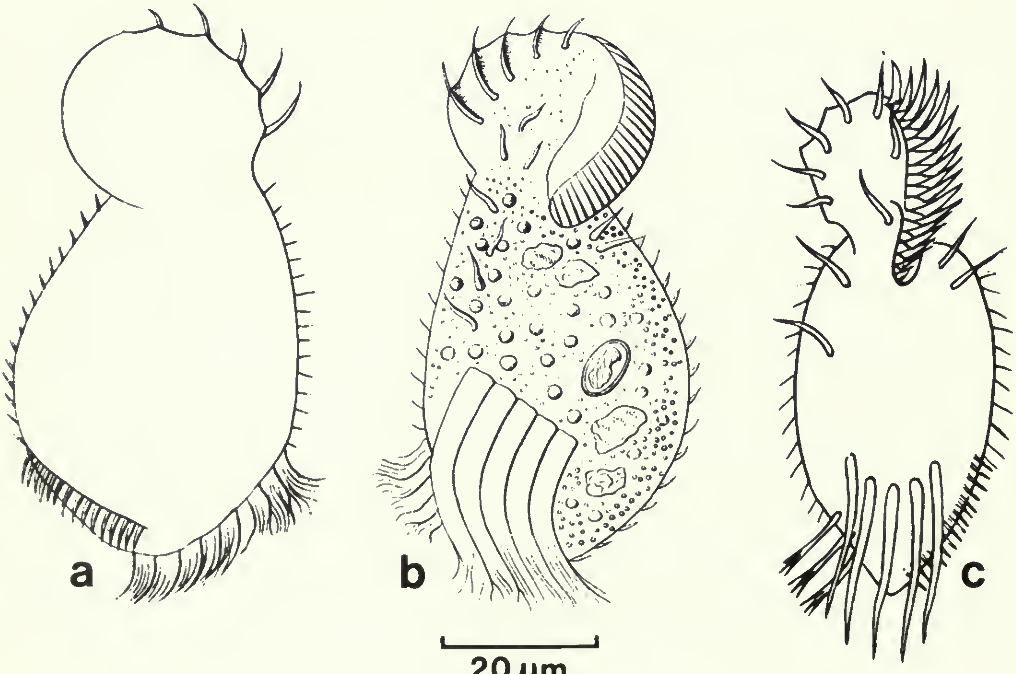

Fig. 1 *Discocephalus rotatorius*: (a, b) after Sauerbrey, 1928 (called *Polycoccon octangulus*); (c) unpublished figure after Fauré-Fremiet (in Dragesco, 1960).

is a row of many (12–20) smaller caudal cirri. The macronucleus is divided into many randomly distributed spherical parts.

Notes. The description is based on that of Sauerbrey (1928) and on the illustration given in Dragesco (1960) but attributed to unpublished diagrams of Fauré-Fremiet.

Discocephalus grandis Dragesco, 1954

Description (Fig. 2). Large (200 µm long) marine species with an uncharacteristically large number (120–150) of ventral cirri arranged in three longitudinal rows: one lies on the left body edge and two on the right. There are 4 frontal cirri which are all located along the right margin of the discoid 'head'. Immediately above the first of the long transverse cirri, on the left, are two small 'satellite' transversal cirri. There are two small right caudal and about 13 left caudal cirri. The macronucleus is divided into many (10–20) spherical parts each being 3–6 µm in diameter.

Note. This description is based on those of Dragesco (1954, 1960) who noted that the species is very similar to *Holosticha discocephalus* Kahl.

Discocephalus ehrenbergi Dragesco, 1960

Discocephalus rotatorius Kahl, 1932 misidentification

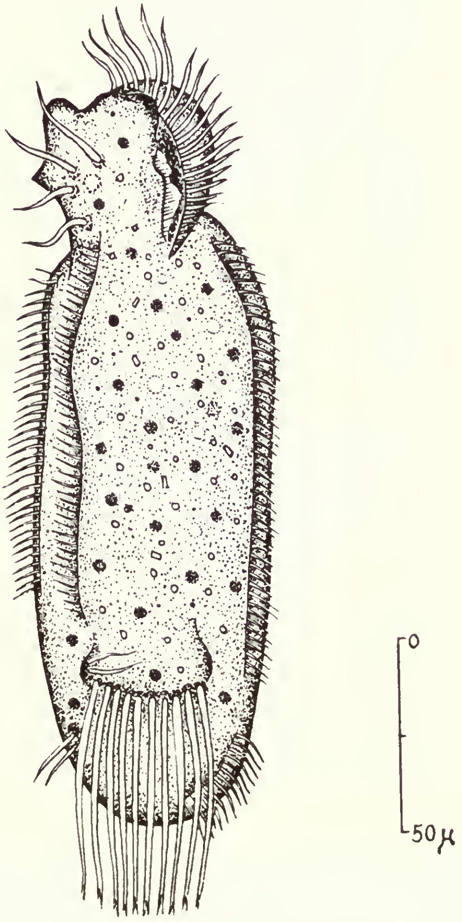

Fig. 2 *Discocephalus grandis*, after Dragesco, 1960.

Description (Fig. 3). This is a medium sized (90–120 µm long) marine species. The presence of 7–9 transverse cirri (with 1 or 2 'satellites', Fig. 3f–h) and 5–7 'pre-membranelles' on the right of the peristome serve to distinguish it from the type species *D. rotatorius* Ehrenberg. The AZM consists of 18–22 membranelles arranged along the left of the peristome and there is an undulating membrane on the right. The 4–8 frontal cirri are of variable size and there are 2 left ventral, 2 mid-ventral and 4 right ventral cirri. The caudal cirri are in two groups: 3–4 right caudal and 14–20 caudal cirri on the left. There are 6 dorsal kineties with only the third from the right extending into the 'head' region (Dragesco, 1965). There is a large

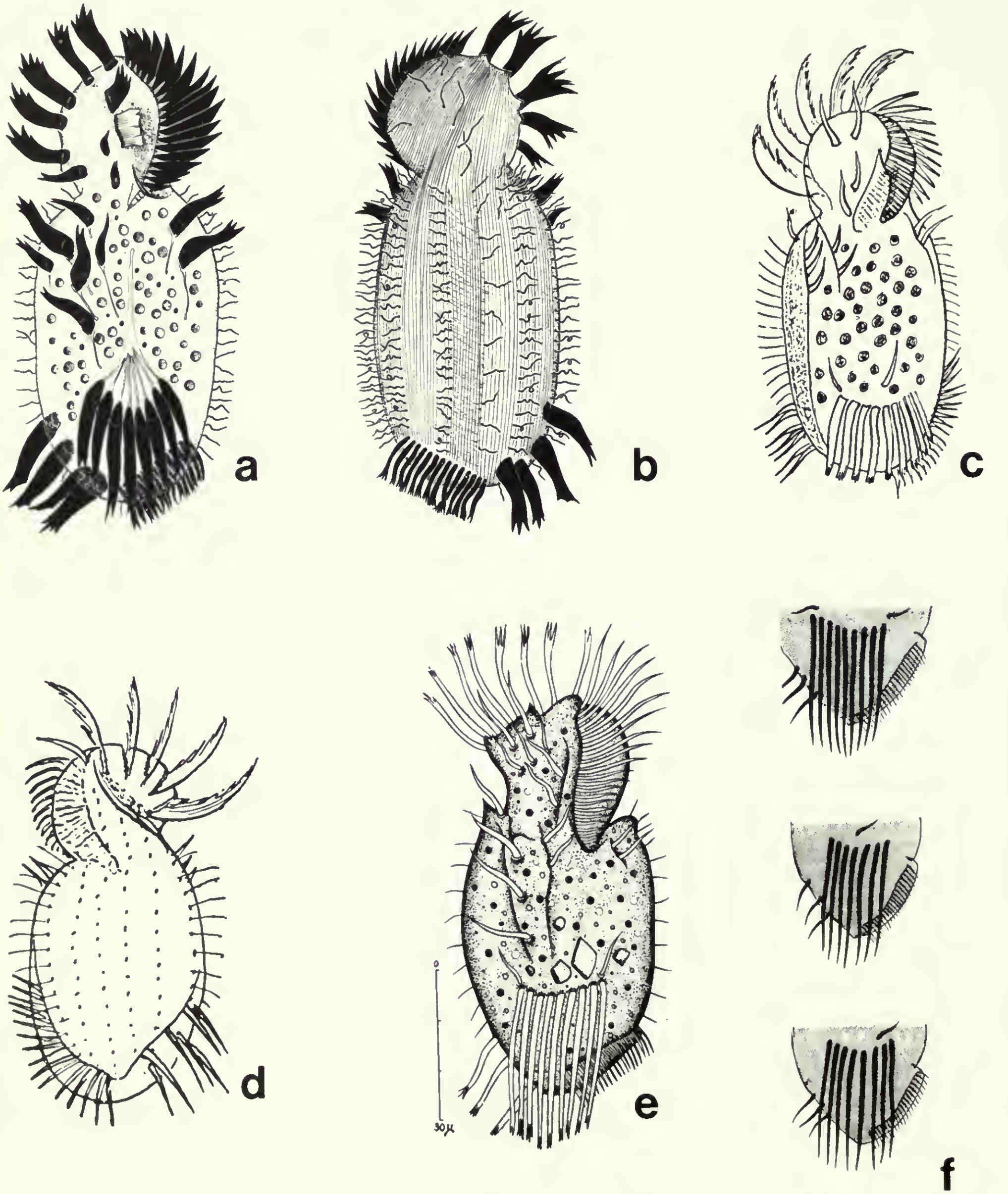

Fig. 3 *Discocephalus ehrenbergi*: (a, b) ventral and dorsal surfaces, after Dragesco, 1965; (c, d) ventral and dorsal surfaces, after Kahl, 1932 (called *D. rotatorius*); (e, f) ventral surface and variations in transverse cirral arrangement, after Dragesco, 1960.

number of spherical parts to the macronuclear apparatus which are scattered throughout the body but apparently not in the 'head' region.

NOTES. This species was first described by Kahl (1932) as *D. rotatorius* Ehrenberg but was renamed and redescribed by Dragesco (1960, 1965). Later Dragesco (1968) expressed doubts about his conclusions and suggested that the species described as *D. ehrenbergi* in 1960 (Fig. 3e–h) might be a different species from that described in 1965 (Fig. 3a–b), although there was insufficient information to be certain. The description above is based on that of Dragesco (1965) but variations noted in other descriptions are included.

Discocephalus minimus Dragesco, 1968

DESCRIPTION. *Discocephalus minimus* (Fig. 4) is characterised by its small size (50–60 µm long) and possession of left ventral cirri. The species has 7 frontal, 4–6 right ventral, 2 mid-ventral and 7 left ventral cirri. There are 4 right caudal and 9–10 left caudal cirri. The macronucleus is divided into relatively few (3–15) spherical parts.

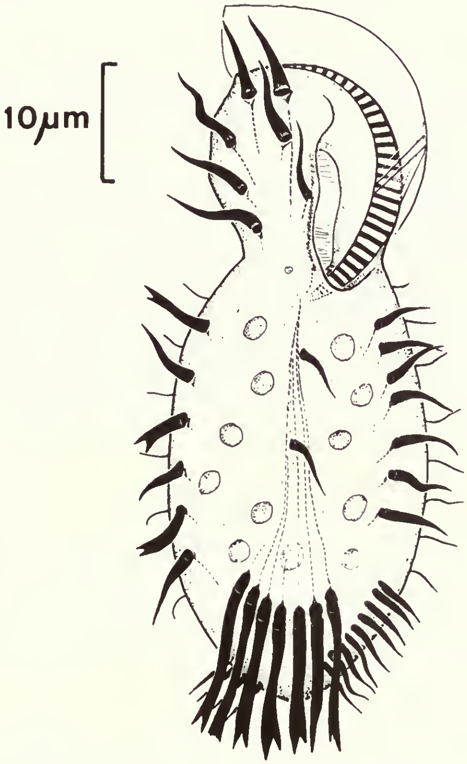

Fig. 4 *Discocephalus minimus*, after Dragesco, 1968.

NOTES. The single description of this species is based on the observation of 5 individuals (Dragesco, 1968) and there are no data on the dorsal aspect of this organism.

Genus ***DIOPHRYS*** Dujardin, 1841

Introduction

It was Dujardin (1841) who first briefly described an organism called *Diophrys marina* and defined the genus *Diophrys* as having a discoid shape with groups of long 'cilia' at the two extremities of the body which was without a mouth. Later Stein (1859*a*) stated that both *D. marina* and the earlier *Stylonychia appendiculata* Ehrenberg, 1838 were synonyms of

Styloplotes appendiculatus Stein, 1859 (see Stein 1859*a*) which he characterised by the presence of three large right caudal cirri. Bütschli (1889) recognised *Diophrys* as a distinct genus and his list of synonyms included certain species of the genera, *Stylonychia* Ehrenberg, *Ploesconia* Dujardin, *Euplotes* Claparède & Lachmann, *Schizopus* Claparède & Lachmann, *Styloplotes* Stein, *Styloplotes* Quennestedt, *Styloplotes* Fresenius, *Styloplotes* Rees, *Styloplotes* Fabre-Domergue, and *Styloplotes* Andrusova. Although Bütschli (1889) stated that there were two species in the genus, he only illustrated *Diophrys* (*Styloplotes*) *grandis* Rees, 1881 and failed to mention *D. appendiculata.* Over the next few years the combination *D. appendiculata* was used occasionally, for example, by Wallengren (1901) and by Calkins (1902) who established the combination *Diophrys* (*Styloplotes*) *appendiculatus* Stein. However, it was Kahl (1932) who first traced the taxonomic history of the species correctly. Borror (1972) recently listed eleven species of the genus with their synonyms and he designated *Diophrys scutum* (Dujardin, 1841) Kahl, 1932 the type species and listed *D. marina* as a synonym of *D. appendiculata* (Ehrenberg) Kahl. In view of the evidence given above, the present authors are of the opinion that *Diophrys* (*Stylonychia*) *appendiculata* (Ehrenberg, 1838) Kahl, 1932 is the correct name and authority for the type species of the genus *Diophrys*.

Kahl (1932) defined the genus *Diophrys* as those members of the family Euplotidae with conspicuous sturdy transverse cirri and a single group of three large caudal cirri. In addition to *D. appendiculata*, Kahl (1932) described, and gave keys, to three other species, *Diophrys* (*Ploesconia*) *scutum* (Dujardin, 1841) Kahl, 1932; *Diophrys hystrix* Buddenbrock 1920 and *Diophrys irmgard* Mansfeld, 1923. Of the eleven species listed by Borror (1972) the present authors accept ten nominal species. *D. tetramacronucleata* Kattar, 1970 and *D. multinucleata* Hartwig, 1973 are two later additions to the genus, characterised by their possession of four and over twenty macronuclei respectively. The authors accept the latter as a distinct species but suspect that the former is a synonym of *D. appendiculata.*

Two of the species, *D. appendiculata* and *D. scutum*, have been described by many authors over the past century but most of the other species are relatively recent additions. In most cases there are rather few data on the extent of intraspecific variation that might be found in potentially useful diagnostic structures. Even so, it was thought worthwhile to present a summary of the data that are available and to discuss the possible diagnostic importance of the various morphological features.

(*a*) *Shape.* The typical body shape of *Diophrys* is an ovoid in which there is often a posterior right lateral indentation where the right caudal cirri are located. The anterior of *D. hystrix* is particularly truncate and the body of *D. kahli* is elongate. The dorsal surface of *Diophrys* is generally smooth, but in *D. irmgard* it is described with a 'trapeziform elevation' (Mansfeld, 1923). These variations are apparently distinctive although the keys here do not rely upon them for identification of these species.

(*b*) *Size.* Most *Diophrys* species are between 50 and 120 µm long. *D. scutum* at 150–200 µm long is the largest and *D. hystrix* at 30–40 µm long is the smallest. Size variation within species appears to be small (Hartwig, 1973) so the size differences between *D. hystrix*, *D. scutum* and *D. appendiculata* (50–100 µm long) are likely to be of diagnostic value.

(*c*) *Adoral zone of membranelles (AZM). Diophrys* has a wide peristome which extends a third to two-thirds down the body length. On the right of the peristome there is a large, wide undulating membrane. On the left, there is a well-developed AZM which continues anteriorly over onto the dorsal surface: in some species it can return to the ventral surface down the right side of the body. Borror (1965*a*) stated that statistical analysis showed that the length of the right portion of the AZM in *D. scutum* was significantly longer from that of *D. peloetes.* He noted that this 'terminal portion' of the AZM in *D. scutum* was 0·4 the body length but only 0·3 the body length in *D. peloetes.* The present authors would not recommend species recognition on such a small difference as this without resort to statistical morphometric analysis but it is a useful feature for distinguishing between certain species.

For example, in *D. appendiculata* the AZM hardly extends onto the right of the body while in *D. scutum* it extends almost to the central region. Rees (1883) and Kahl (1932) also consider this right extension of the AZM to be an important diagnostic feature by which they identified *Styloplotes quennerstedti* and *D. scutum* respectively.

(*d*) *Cirri.* The type species, *D. appendiculata*, has 7–8 frontoventral, 5 transverse, 1–3 left marginal and 3 right caudal cirri. The frontoventral cirri are arranged in two distinct groups, with 5 in the anterior right frontal group and 2–3 in the ventral group, often much smaller than the frontal cirri, lying in close proximity to the first transverse cirrus on the right. This distribution pattern is seen in all species but *D. hystrix*, *D. irmgard* and *D. kahli* have 9–10 frontoventrals in groups of 7 frontals and 2–3 ventrals which the authors consider to be of diagnostic importance. Some authors are in agreement with this others are not. For example, Agamaliev (1967) established a new species *D. scutoides* which differs from *D. scutum* only in having five instead of seven frontoventral cirri. However, Borror (1963) identified an organism as *D. irmgard* even though it possessed only five frontoventrals rather than the nine in Mansfeld's (1923) original description. Borror (1963) neither established the organism as a new species nor did he suggest the cirral difference to be due to intraspecific variation. The morphogenesis of cirri in *D. appendiculata* was described by Wallengren (1901). The frontoventral-transverse cirri arise from six streaks of kinetosomes as in *Euplotes*, with the I/1, II/2, II/3, III/2 and IV/2 cirri forming the frontals: V/2 and VI/2 the ventrals and II–VI/1 the transversals (Fig. 5).

The transverse cirri of *Diophrys* are noticeably larger than those of *Euplotes*. There are almost invariably five transverse cirri but there are only four in *D. irmgard* and *D. multinucleata*. The presence of large, sickle-shaped, dorso-laterally attached right caudal cirri is a characteristic feature of the genus *Diophrys*. During morphogenesis, these cirri arise from basal bodies at the posterior ends of the ciliary rows on the right of the dorsal surface (Borror, 1972). Most of the species described have three of these cirri but *D. quadricaudatus* Agamaliev, 1967 has four and *D. kahli* Dragesco, 1963 has only one. Intraspecific variation in the number of these cirri has not yet been reported and so it is thought that this might be a useful diagnostic character. In most species, the left marginal cirri are located just posterior

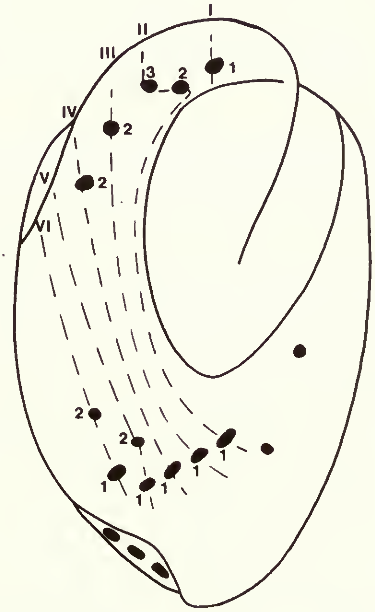

Fig. 5 Arrangement and numbering of cirral streaks in *Diophrys appendiculata*, after Wallengren, 1901.

to the peristome, but in *D. irmgard*, *D. kahli* and *D. multimicronucleata*, they are in the 'caudal position' as are those in *Euplotes* and *Uronychia.* Hartwig (1974) believed that the positioning of these cirri in these three species was sufficient to constitute a separate genus. While the present authors agree that the caudal positioning of the left marginal cirri appears to be a significant character apparently associated with the presence of only four transverse cirri, they hesitate to erect a new genus on this alone. Mansfeld (1923) and Kahl (1932) distinguished *D. irmgard* from other species, not by the position of the left marginal cirri but by their number. Although most species have two left marginal cirri and *D. irmgard* has three, variation between 1–3 has been observed in *D. appendiculata.*

(*e*) *Nuclear features.* The most commonly found nuclear arrangement in *Diophrys* is two macronuclei and 2–6 micronuclei. Exceptions to this include *D. quadricaudatus*, *D. tetramacronucleata* and *D. multinucleata* which have three, four and over 20 macronuclei respectively, with the diagnosis of the latter two species resting heavily on this feature. The macronuclei may be rod-shaped, ovoid or moniliform.

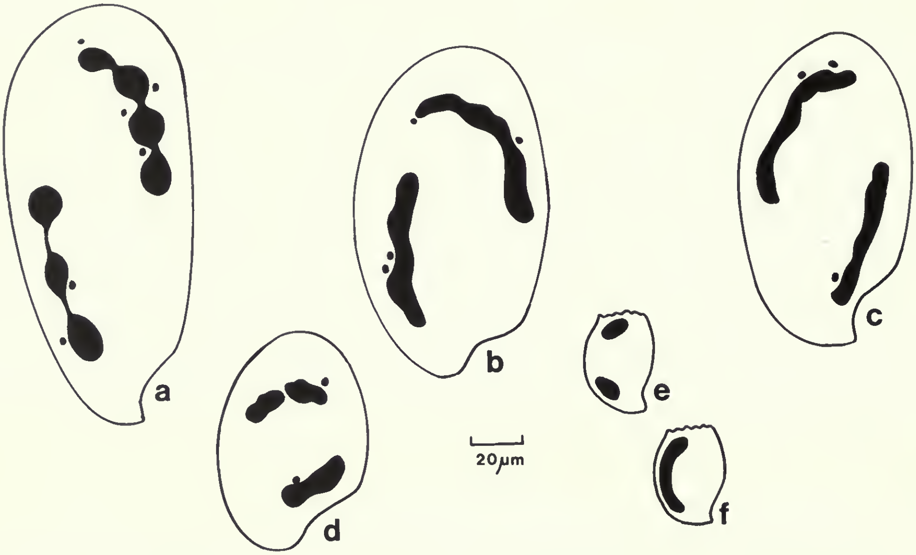

Fig. 6 Nuclear arrangement in *Diophrys*: (a) *Diophrys magnus*, after Raikov & Kovaleva, 1968; (b–d) *Diophrys scutoides*, after Agamaliev, 1967; (c) *Diophrys quadricaudatus*, after Agamaliev, 1967; (e, f) *Diophrys hystrix*, after Buddenbrock, 1920.

Raikov and Kovaleva (1968) separated *D. magnus* from *D. scutum* principally on the basis of its macronuclei being moniliform, however they are similar to those of *D. scutum* and other species which are often shown to be slightly nodular (Fig. 6a–c). Here *D. magnus* and *D. scutum* are therefore regarded to be synonymous.

Summers (1935) described the reorganisation and division of the macronuclei of *D. scutum*, misidentified as *D. appendiculata.* He noted (Fig. 7) that in the normal resting stage, the species possesses two macronuclei without a visible strand between them and a variable number of micronuclei. He observed that fragmentation of the reorganised parts of the macronuclei was not uncommon but 'fragments of the macronuclei have never been found free in the cytoplasm after the several parts fuse to form the rod-like mass'. One cannot be certain if the tripartite macronuclear structure of *D. quadricaudatus* (Fig. 6d) is the result of fragmentation or if it is the true resting stage, but it is likely that the sausage-shaped nucleus which Buddenbrock (1920) described in certain specimens of *D. hystrix* to be a divisional stage in the normally ovoid macronuclei (Fig. 6e).

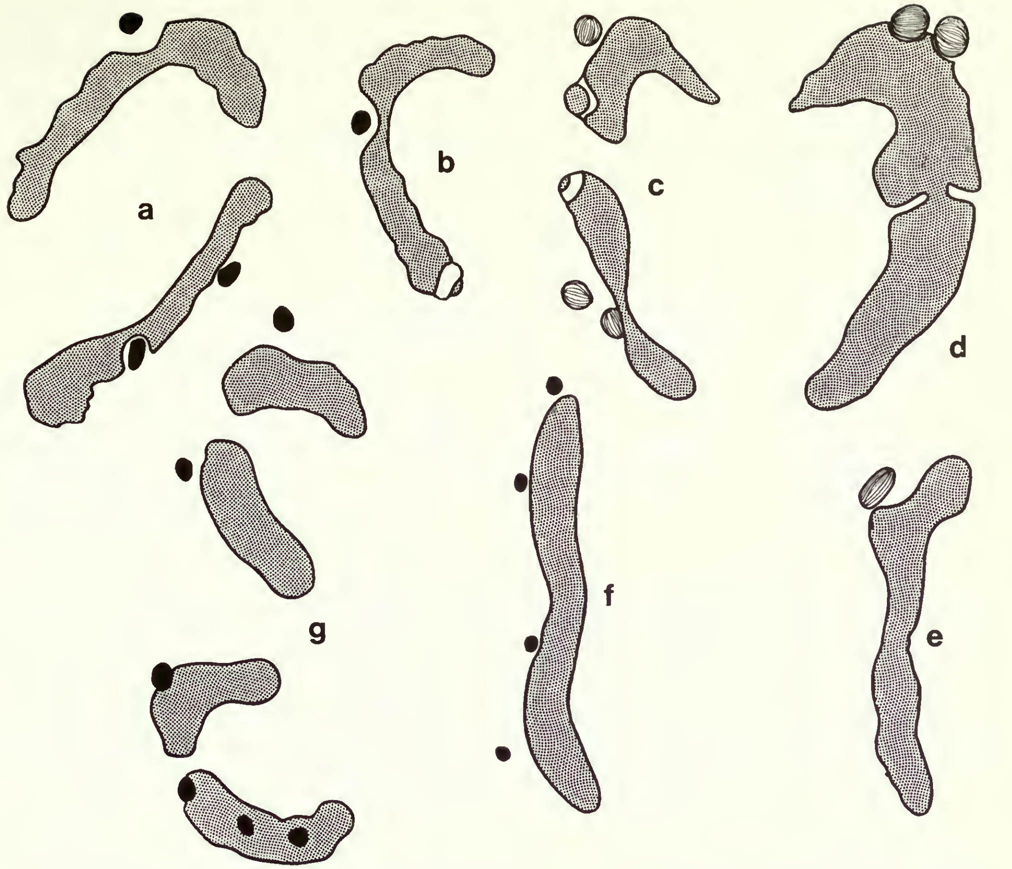

Fig. 7 Division of the macronucleus of *Diophrys scutum*, after Summers, 1935 (called *D. appendiculata*): (a) nucleus at rest; (b) first appearance of a reorganisation band at the outer pole of the posterior macronucleus; (c) reorganisation bands about to disappear at inner poles of the macronuclei; (d) fusion of the macronuclei; (e) after fusion; (f) macronucleus beginning to divide; (g) macronuclei completely divided just before daughter cells separate.

Kisselbach (1936) also illustrated various stages in the nuclear development of *D. appendiculata* (Fig. 8a–e) one of which shows a quadripartite stage similar to that illustrated by Kattar (1970) in *D. tetramacronucleata* (Fig. 8f, g). In view of this *D. tetramacronucleata* should be strongly suspected as being a synonym of the type species. However, since one illustration by Kattar (1970) and another by Hartwig (1974) show the four ovoid macronuclei to be completely distinct (Fig. 8g) the species has been provisionally included here awaiting further data. As mentioned above, there are commonly 2–6 micronuclei in *Diophrys*. Borror (1965*a*) accorded little significance to this feature and referred to Ito (1963) who stated that macronuclei may vary considerably in number within a species.

(*f*) *Dorsal silver-line system*. Borror (1965*a*) pointed out that few workers had mentioned the dorsal ciliature in *Diophrys* species descriptions and observed that Kahl (1932) was the first to note the presence of five rows of short cilia in *D. scutum*. Using the Chatton-Lwoff (1930) technique, Borror (1965*a*) was able to show that '... the kinetosomes in the dorsal rows of *Diophrys* behave during cell division in a manner similar to the behavior of the dorsal kinetosomes in *Euplotes*, hence the proter and opisthe usually have the same number of rows. Within a population, with practically no exceptions, all members of the genus present have the same number of rows of cilia dorsally, and this is apparently not related with body size.'

Several authors have used the number of dorsal kineties as a diagnostic character (Borror, 1965*a*, *b*: Agamaliev, 1967: Raikov & Kovaleva, 1968). However, the dorsal silver-line systems of other species including *D. hystrix*, *D. irmgard*, *D. kahli*, *D. tetramacronucleata* and *D. multinucleata* still remain to be described. For this reason the key here only distinguishes between *D. oligothrix* and *D. peloetes* on this character. All dorsal argyromes that have been described so far consist of a meshwork pattern and are therefore of little value for specific identification.

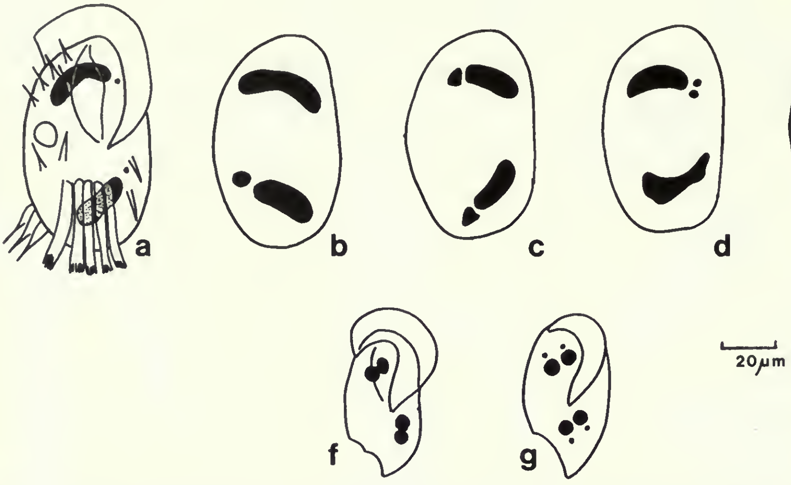

Fig. 8 Nuclear arrangement in *Diophrys*: (a–e) *Diophrys appendiculata*, after Kisselbach, 1936; (f, g) *Diophrys tetramacronucleata*, after Kattar, 1970.

Diagnosis of *Diophrys*

Marine hypotrichs 30–200 μm in length. Ovoid body usually with prominent right posterio-lateral concavity from which arise three large sickle-shaped right caudal cirri. There are 5–10 frontoventral, 4–6 transverse and usually 2–3 left marginal cirri. There are often two elongate, sometimes nodular, macronuclei but in some species there may be four or over twenty macronuclei. There is a variable number of micronuclei. The dorsal silver-line system consists of 4–8 dorsolateral kineties and a mesh-like argyrome.

Key to the species of *Diophrys*

1	With 5 frontoventral cirri	***D. scutoides***
	With more than 5 frontoventral cirri	2
2	With 7–8 frontoventral cirri	3
	With 9–10 frontoventral cirri	10
3	With 4 right caudal cirri	***D. quadricirratus***
	With 3 right caudal cirri	4
4	With 1–3 left marginal cirri	5
	Without left marginal cirri	***D. salina***
5	With 2 macronuclei	6
	With 4 or more macronuclei	9
6	With 5–6 dorsolateral kineties	7
	With less than 5 or greater than 6 dorsolateral kineties	8
7	AZM extends almost to centre of right border, 150–200 μm long	***D. scutum***
	AZM hardly extends at all down right border, 50–100 μm long	***D. appendiculata***
8	With 4 dorsolateral kineties	***D. oligothrix***
	With 8 dorsolateral kineties	***D. peloetes***

9	With 4 macronuclei	*D. tetramacronucleata*
	With 20 or more macronuclei	*D. multinucleata*
10	With 2 left marginal cirri posterior to the peristome, 30–40 µm long	*D. hystrix*
	Left marginal cirri in the 'caudal' position, 80–100 µm long.	11
11	With 1 right caudal and 2 left marginal/caudal cirri	*D. kahli*
	With 3 right caudal and 3 left marginal/caudal cirri	*D. irmgard*

Species descriptions

Diophrys appendiculata (Ehrenberg, 1838) Kahl, 1932

Stylonychia appendiculata Ehrenberg, 1838
Diophrys marina Dujardin, 1841
Schizopus norwegicus Claparède & Lachmann, 1858
Styloplotes appendiculatus Stein, 1859
Styloplotes fresenii Rees, 1883
Styloplotes appendiculatus var. *pontica* Andrusova, 1886
Planiplotes wagneri Andrusova, 1886
Diophrys appendiculatus (Stein, 1859) Calkins, 1902

DESCRIPTION (Figs 9, 10). This, the type species of the genus, is 50–100 µm long. The body shape is typically ovoid with the characteristic lateral concavity at the posterior where the three sickle-shaped right caudal cirri arise. There are 7–8 frontoventral cirri – 5 anterior and 2–3 close to the transversals, 5 transverse and 1–3 left marginal cirri. The AZM extends down half to two-thirds of the length of the body on the left but hardly at all on the right. The two macronuclei are usually elongate to ovoid and may be smooth or nodular. There are 2–4 micronuclei and 5–6 dorsolateral kineties each carrying 6–10 cilia.

NOTES. Some of the nomenclatural history of this species has already been outlined in the introduction to the genus. Kahl (1932) transferred *Stylonychia appendiculata* Ehrenberg, 1838 to the genus *Diophrys* and redescribed the species. However, he made no reference to the fact that Stein (1859*a*) had already erroneously redefined the species as *Styloplotes appendiculatus* which combination was subsequently used by many workers (Fresenius, 1865: Quennerstedt, 1867: Kent, 1881: Rees, 1883: Fabre-Domergue, 1885). Stein (1859*a*) suggested that Ehrenberg (1838) had overlooked the frontoventral cirri and suggested that *Schizopus norwegicus* Claparède & Lachmann, 1858 was probably a synonym, even though Claparède & Lachmann (1858) had distinguished their species from *Stylonychia appendiculata* Ehrenberg by the absence of marginal cirri. It seems likely that the two left marginal cirri were mistaken identified to be satellite transverse cirri. Calkins (1902) later transferred *Styloplotes appendiculatus* Stein to the genus *Diophrys*.

Rees (1883) briefly described a species of *Styloplotes* which he stated was the same as *Styloplotes appendiculatus* Stein as described by Fresenius (1865) which he (Rees, 1883) proceeded to call *Styloplotes fresenii*. Earlier Rees (1881) had described the new species *Styloplotes grandis* but later (Rees, 1883) concluded that it was identical to *Styloplotes norwegicus* Quennerstedt, 1867 which he then erroneously called *Styloplotes quennerstedti*. In the present authors, opinion, Quennerstedt (1867) was mistaken in making *Styloplotes norwegicus* Quennerstedt a synonym of *Schizopus norwegicus* Claparède & Lachmann. It is here considered that the former species is a synonym of *D. scutum* because of the extent to which the AZM is developed on the right side of the body. Rees (1883) also used this character to distinguish *Styloplotes quennerstedti*, a synonym of *D. scutum*, from *Styloplotes fresnii*, a synonym of *D. appendiculata*.

Diophrys scutum (Dujardin, 1841) Kahl, 1932

Ploesconia scutum Dujardin, 1841 (in part)

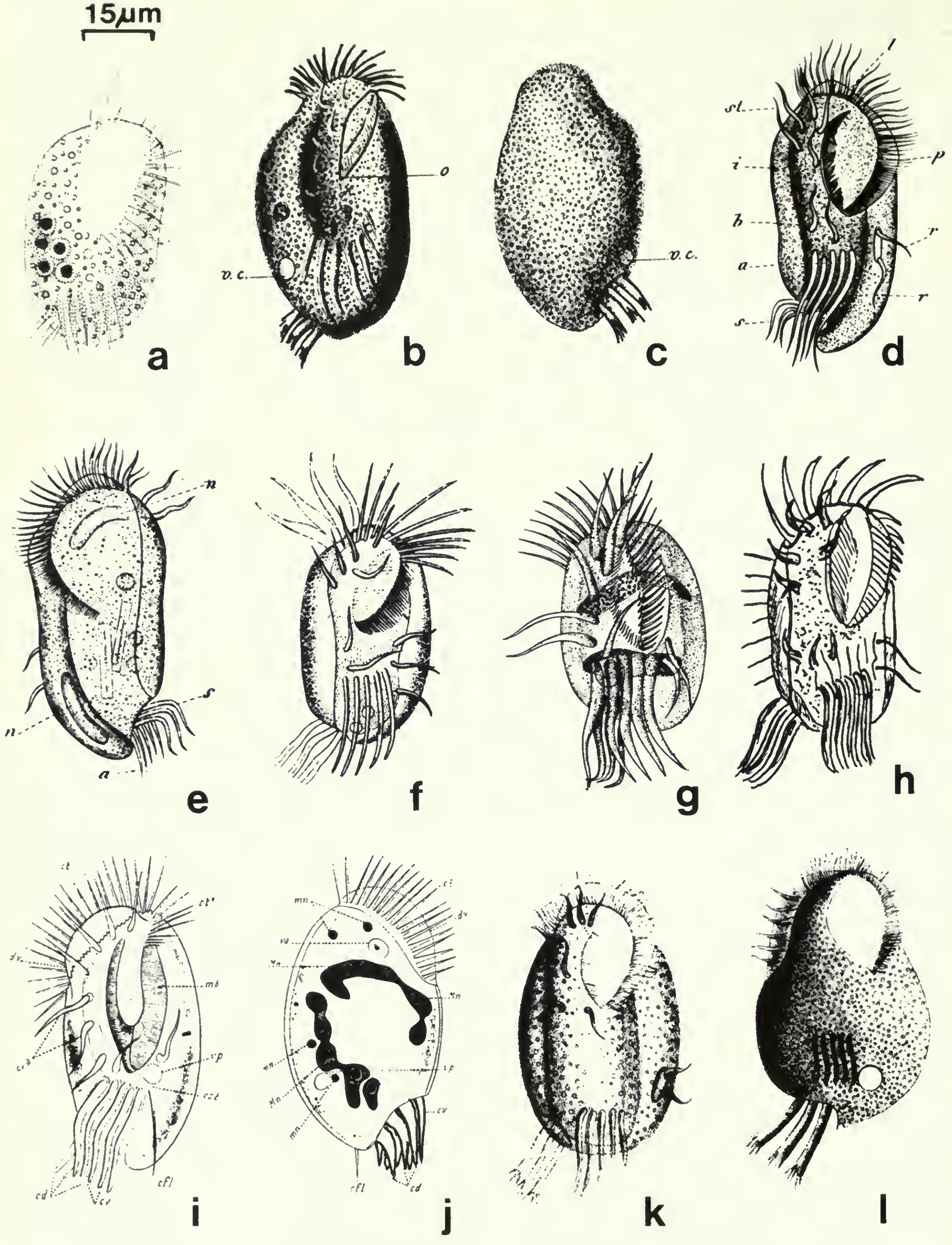
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Fig. 9 *Diophrys appendiculata*: (a) after Ehrenberg, 1838 (called *Stylonychia appendiculata*); (b, c) after Claparède & Lachmann, 1858 (called *Schizopus norwegicus*); (d, e) after Stein, 1859*a* (called *Styloplotes appendiculatus*); (f) after Fresenius, 1865 (called *Styloplotes appendiculatus*); (g) after Calkins, 1902 (called *D. appendiculatus*; (h) after Kahl, 1932; (i, j) after Pierantoni, 1909; (k) after Andrusova, 1886 (called *Styloplotes appendiculatus* var. *pontica*; (l) after Andrusova, 1886 (called *Planiplotes wagneri*).

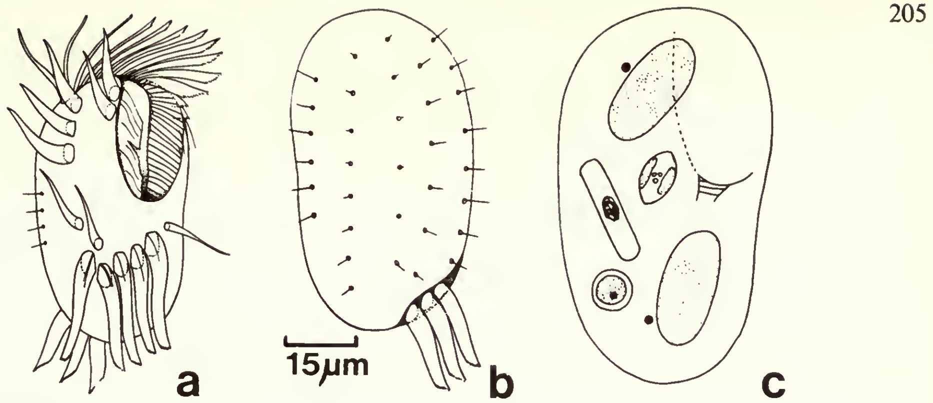

Fig. 10 *Diophrys appendiculata*, after Borror, 1963: (a) ventral surface; (b) dorsal surface; (c) nuclei.

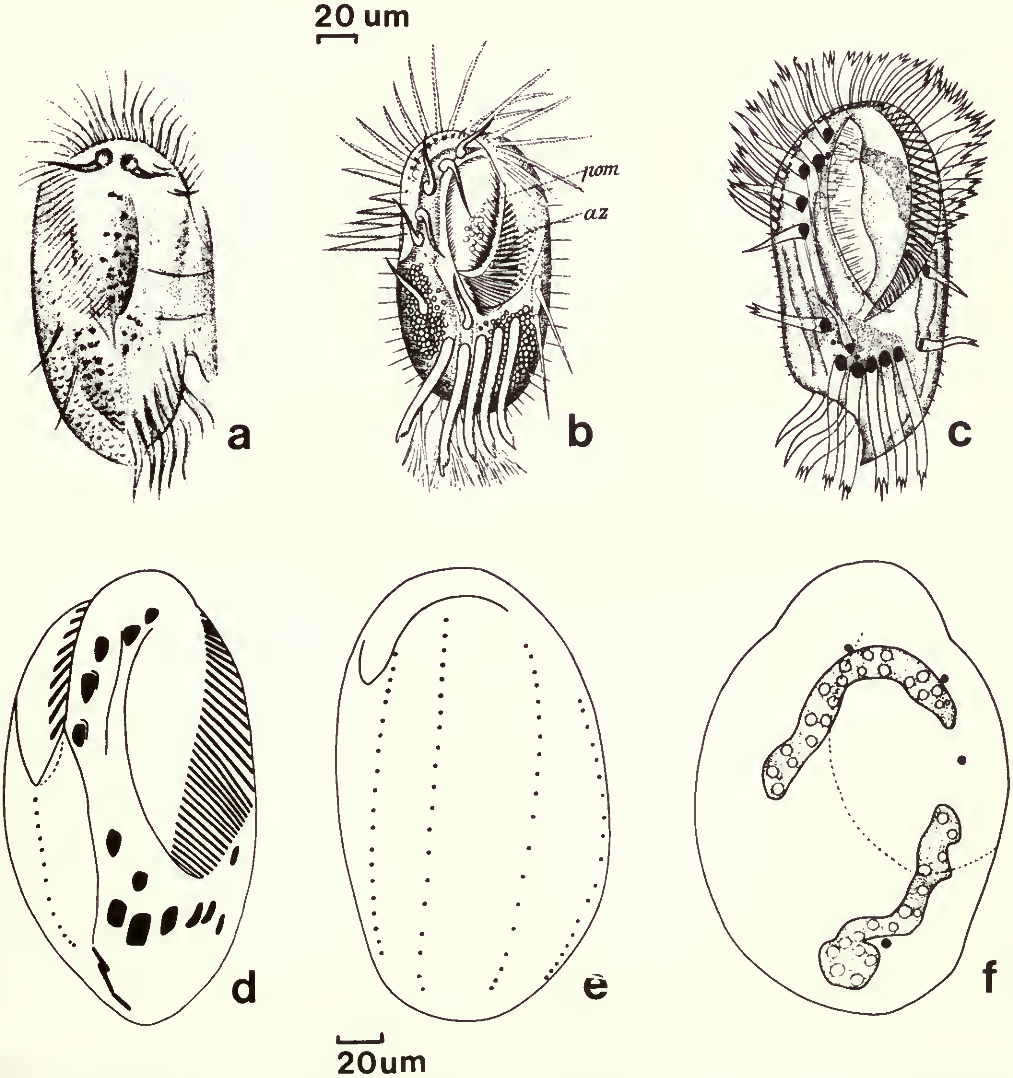

Fig. 11 *Diophrys scutum*: (a) after Dujardin, 1841 (called *Ploesconia scutum*); (b) after Butschli, 1889 (called *Diophrys grandis*); (c) after Dragesco, 1963; (d–f) ventral surface, dorsal surface, and nuclei, after Borror, 1965*a*.

Styloplotes norwegicus Quennerstedt, 1867
Styloplotes grandis Rees, 1881
Styloplotes quennerstedti Rees, 1883
Diophrys grandis Butschli, 1889
Diophrys magnus Raikov & Kovaleva, 1968
Diophrys kasymovi Agamaliev, 1971

Description (Figs 11, 12). This is the largest species (150–200 µm long) of the genus so far described. It may be distinguished from the type species, *D. appendiculata*, by its size and by the AZM which extends to the central body region on the right side. The body shape is ovoid with an indentation in the posterior right. The dorsal surface is smooth and arched. There are 3 large sickle-shaped right caudal cirri, 7–8 frontoventral, 5 transverse and 2 left marginal cirri. The two elongate macronuclei may be curved, nodular or moniliform and are accompanied by up to six micronuclei. The dorsal silver-line system consists of 5–6 dorsolateral kineties interspersed with mesh-like argyromes.

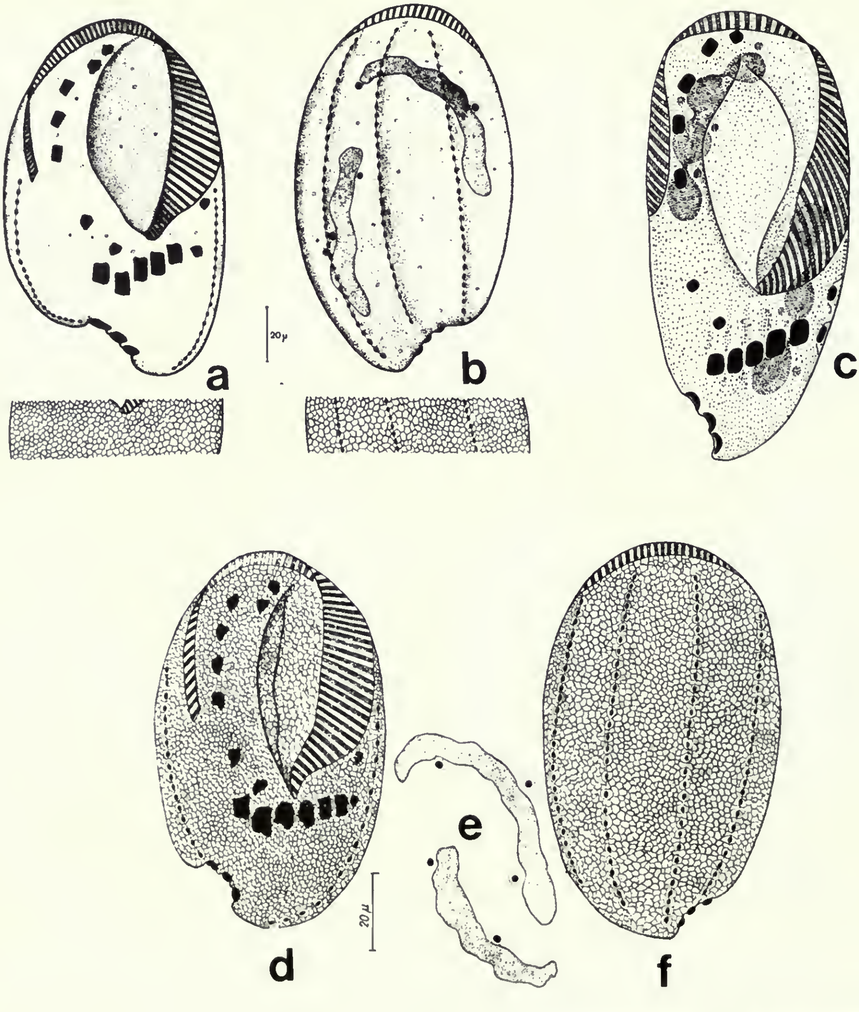

Fig. 12. *Diophrys scutum*: (a, b) ventral and dorsal surfaces with section showing argyromes, after Agamaliev, 1968; (c) after Raikov & Kovaleva, 1968 (called *D. magnus*); (d, f) ventral argyrome, nuclei and dorsal argyrome after Agamaliev, 1971 (called *D. kasymovi*).

Notes. Claparède & Lachmann (1858) and Stein (1859*a*) believed that the three illustrations of *Ploesconia scutum* by Dujardin (1841) were of two different species. Claparède & Lachmann (1858) thought that one represented a *Euplotes* species whereas Stein (1859*a*) considered it to be *Styloplotes appendiculatus* Stein. The present authors doubt both of these opinions but agree with Kahl (1932) who identified the species as *Diophrys scutum* and considered the AZM originating in the middle of the right border to be an important diagnostic feature. It is mainly by this character that *D. scutum* can be distinguished from *D. appendiculata*. Raikov and Kovaleva (1968) distinguished *D. magnus* from *D. scutum* by the difference in the shapes of their macronuclei which is not a significant feature. The recent addition *D. kasymovi* Agamaliev, 1971 has been included here in spite of it being rather small for this species.

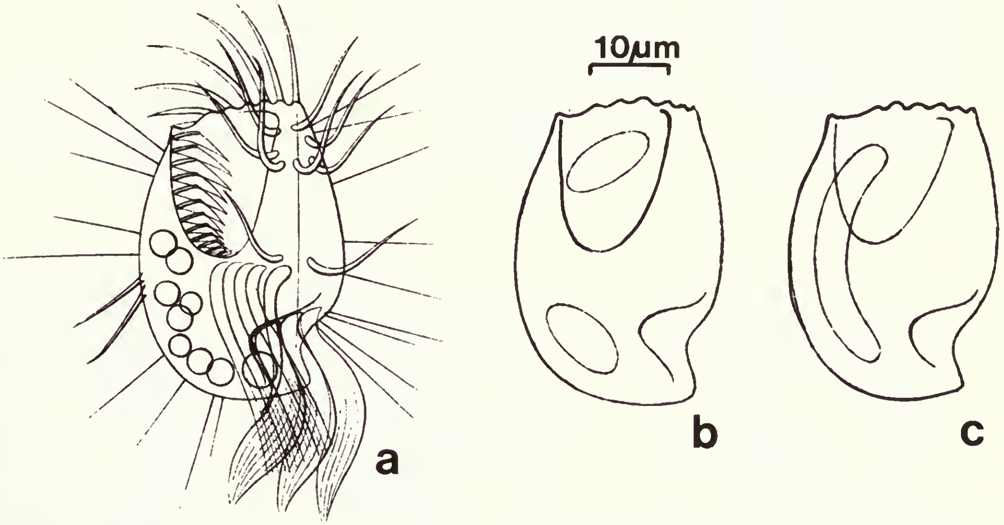

Fig. 13 *Diophrys hystrix*, after Buddenbrock, 1920: (a) ventral surface; (b, c) nuclear features.

Diophrys hystrix Buddenbrock, 1920

Description (Fig. 13). *Diophrys hystrix* is a small (30–40 µm long) species. The body outline is generally oval but it is truncated anteriorly and there is the usual concavity on the posterior right accommodating three large sickle-shaped right caudal cirri. The dorsal surface is strongly arched. The ten frontoventral cirri are arranged in two distinct groups with 7 'frontals' at the anterior on the right of the peristome and 3 'ventrals' near the transverse cirri. One of the 'ventrals' is adjacent and similar in size to the transversals, but it points in the opposite direction and is used in the creeping movements of the animal. There are 4 long transverse cirri and 2 small left marginal cirri located just behind the peristome. There are two ovoid macronuclei.

Notes. Kahl (1932) gave an almost identical description and illustration of this species as in Buddenbrock's (1920) original. Kattar (1970) identified a small (35–40 µm) species with two ovoid macronuclei as *D. hystrix* but this is a dubious identification since the author gave an inadequate description and the illustration was of a different shape and cirral number to that of Buddenbrock (1920).

Diophrys irmgard Mansfeld, 1923

Description (Fig. 14). This is a medium sized (75–135 µm long) marine species. The body shape is characteristic, being broadly oval in outline but tending to be rectangular. The wide peristome is approximately half the body length and there is a prominent undulating

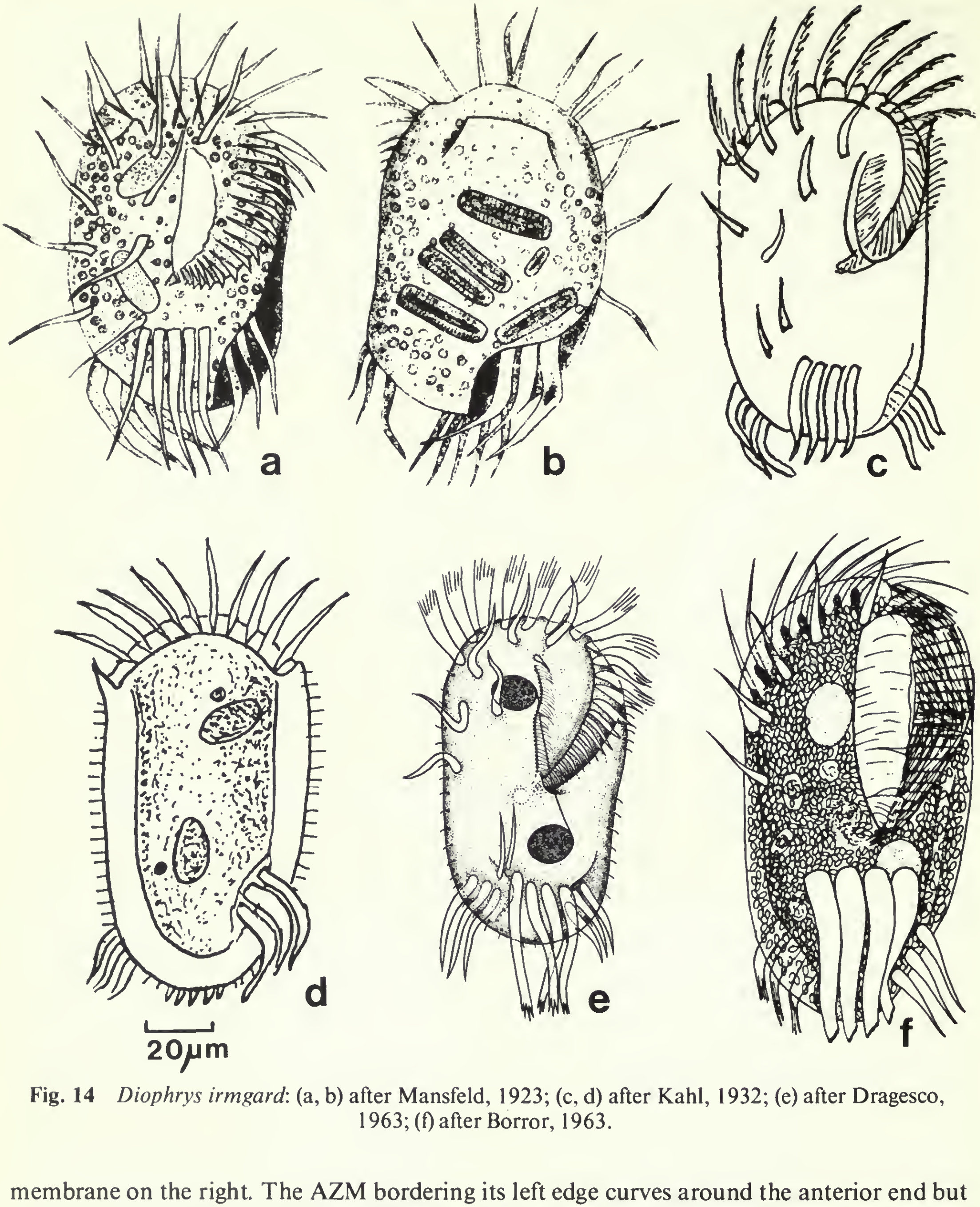

Fig. 14 *Diophrys irmgard*: (a, b) after Mansfeld, 1923; (c, d) after Kahl, 1932; (e) after Dragesco, 1963; (f) after Borror, 1963.

membrane on the right. The AZM bordering its left edge curves around the anterior end but only just extends to the right side of the body. There are 3 right caudal, 9 frontoventral, 4–5 transverse and 3 left marginal cirri. The two ovoid macronuclei are 8 µm in diameter and each is associated with a micronucleus.

NOTES. This species may be distinguished from the type species, *D. appendiculata*, by the presence of 9 instead of 7 frontoventral cirri and because the left marginal cirri are in the 'caudal' position. The shape of its body is consistently observed to be widely oval, rectangular and lacks the posterior lateral concavity on the right which is usually characteristic of the genus. Additionally, the right caudal cirri are attached dorsally like those of *Uronychia*. Borror (1963) described an organism which he called *D. irmgard* but as it had only 5 frontoventral cirri perhaps future studies will show this to be a separate species.

Diophrys salina Ruinen, 1938

Description (Fig. 15). This is a small (30–40 μm long) species. The outline shape of the body is characteristically oval without any obvious lateral concavities but there is a posterior indentation where the 3 large caudal cirri arise. The dorsal surface is strongly convex, but the ventral surface is flattened. The peristome region extends to the centre of the body, with an AZM on the left and a well developed undulating membrane on the right. The frontoventral cirri are arranged in two groups with 4 right anterior 'frontals' and 4 'ventrals' situated immediately behind, and to the right of, the peristome. There are no left marginal cirri. Five transverse cirri lie between the caudal and 'ventral' cirri. The original description did not include any details concerning the nuclear apparatus. Feeds on diatoms, algae and bacteria.

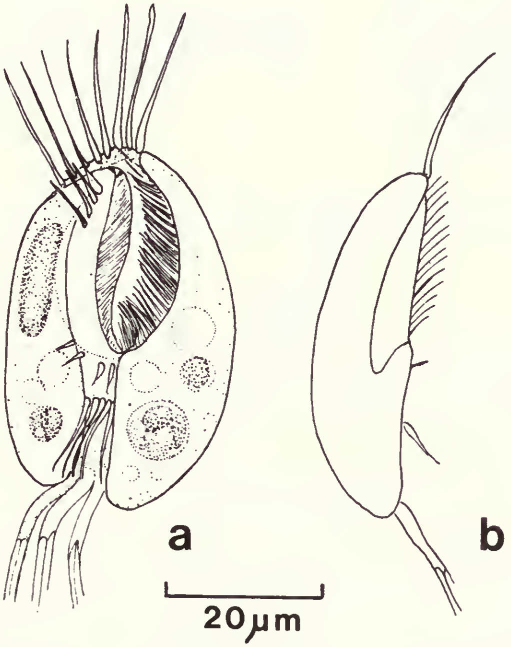

Fig. 15 *Diophrys salina*: (a, b) ventral surface and lateral view, after Ruinen, 1938.

Diophrys kahli Dragesco, 1963

Description (Fig. 16). This species is about 80 μm long, the body is elongate with a short posterior narrowed tail region. The peristome is small, bordered on the right by a well developed undulating membrane and on the left by a small AZM. The frontoventral cirri consist of a group of 7 long 'frontals' and 2 small 'ventrals'. The 5 transverse cirri are long, the 2 left marginal cirri are in the 'caudal' position and there is only one right caudal cirrus. The two oval macronuclei are connected by a nuclear membrane and there are 4–6 micronuclei. A few cilia have been observed along the left border of the animal.

Notes. Dragesco (1963) identified an organism that he considered to be identical to one incompletely studied by Kahl (1932) which he called *D. kahli*. Untypically, the body of this species is rather elongate and its left marginal cirri emerge caudally instead of immediately posterior to the peristome. Hartwig (1974) grouped this species with *D. irmgard* and *D.*

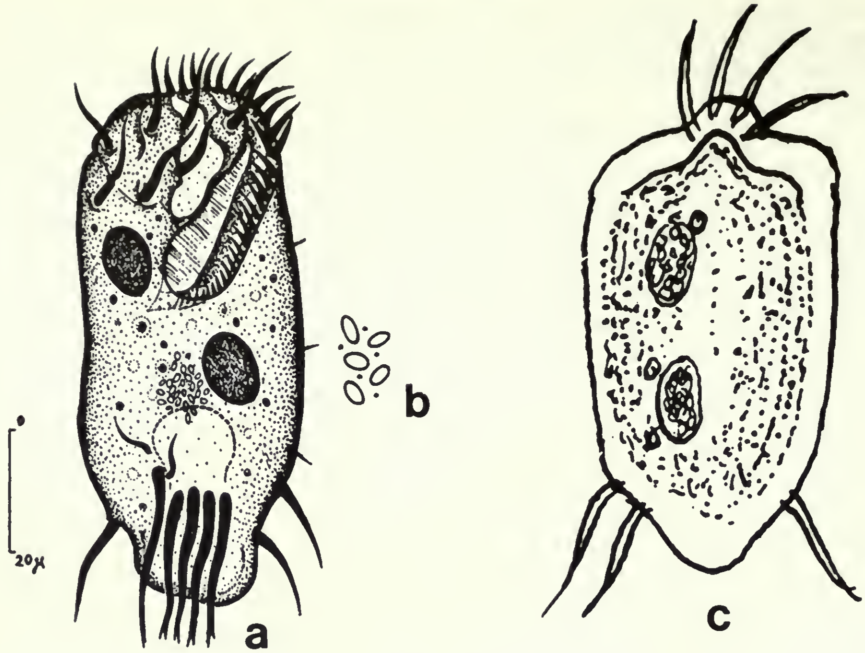

Fig. 16 *Diophrys kahli*: (a, b) ventral surface and dorsal plaques, after Dragesco, 1963; (c) dorsal surface, after Kahl, 1932 (called an 'incompletely studied *Diophrys* species').

multinucleata because of this latter feature. In contrast to other species in the genus, *D. kahli* has only one right caudal cirrus, its peristome is rather small and the AZM is underdeveloped. Dragesco (1963) described the presence of small oval plaques on the dorsal surface (Fig. 14b) which he suspected to be 'protrichocysts'.

Diophrys oligothrix Borror, 1965

Description (Fig. 17). *Diophrys oligothrix* is a medium sized (79–106 μm long), ovoid species. The concavity at the posterior right edge, so typical of the genus, is here inconspicuous and the dorsal surface smooth. The AZM bordering the left edge of the large peristome continues dorsally along the anterior region to the right side of the body. The ciliature and nuclear features are also typical of the genus, there are 7 frontoventral, 5 transverse, 2 left marginal and 3 right caudal cirri. The two irregular, elongate macronuclei are usually accompanied by four micronuclei. The silver-line system consists of 3 dorsal kineties, one lateral kinety on the right and a fine mesh-like argyrome. The dorsal kineties bear, from left to right, 13–20, 16–24, 12–18 cilia and the ventral kinety 9–13 cilia.

Note. This species is distinguished from *D. scutum* on the basis of its different number of kineties.

Diophrys peloetes Borror, 1965

Description (Fig. 18). *D. peloetes* is a medium sized (95–135 μm long) species typical of the genus. It has a wide peristome which is about two-thirds of the body length, bordered by a well developed AZM on the left and an undulating membrane on the right. The AZM travels along the anterior dorsal edge onto the right side of the body where it extends about 3/10 of the body length. There are 3 prominent right caudal cirri, 5 long transverse, 7 frontoventral and 2 left marginal cirri. The two macronuclei are elongate. There are 8 dorsolateral

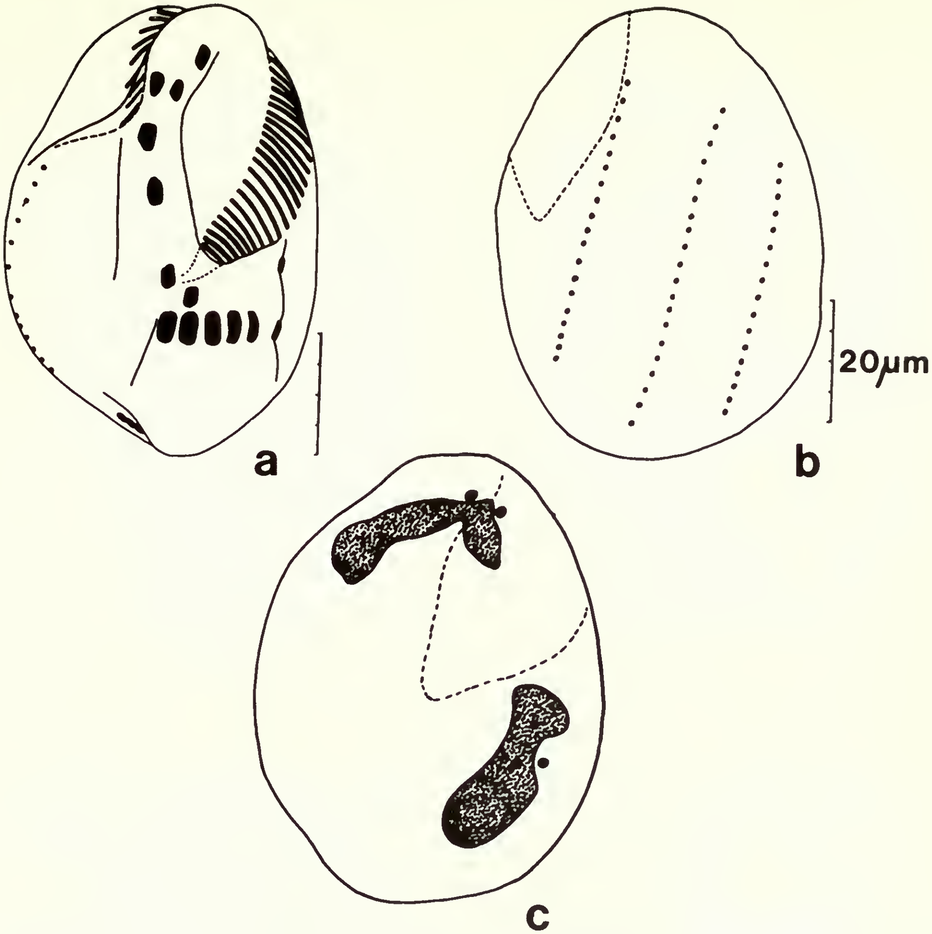

Fig. 17 *Diophrys oligothrix*, after Borror, 1965*b*: (a) ventral surface; (b) dorsal surface; (c) frontal section showing nuclei.

kineties, each bearing 6–17 cilia. The number of kineties distinguishes this species from *D. scutum* which has only five.

NOTES. Borror (1965*a*) established *D. peloetes* after a morphometric comparison with *D. scutum*. He stated that the new species was 'extremely similar to *D. scutum* except for having eight dorsal rows of cilia instead of five, having fewer cilia per row, and having a significantly shorter AZM'. He also pointed out that he had identified it incorrectly as *D. scutum* in an earlier study (Borror, 1963).

Diophrys quadricaudatus Agamaliev, 1967

DESCRIPTION (Fig. 19). This is a medium sized (100–110 µm long) species, characterised by the presence of 4 right caudal cirri arising from a particularly prominent concavity on the posterior right of an otherwise oval body. The wide peristome is about 48 µm long and on its right there is a conspicuous undulating membrane. The AZM is composed of 50–60 membranelles which extend forward over to the right side of the body. There are 7 frontoventral, 5 transverse, and 3 left marginal cirri. The dorsal silver-line system consists of 5 or 6 dorsolateral kineties and a finely-meshed dorsal argyrome. There are two anterior and one posterior macronuclei.

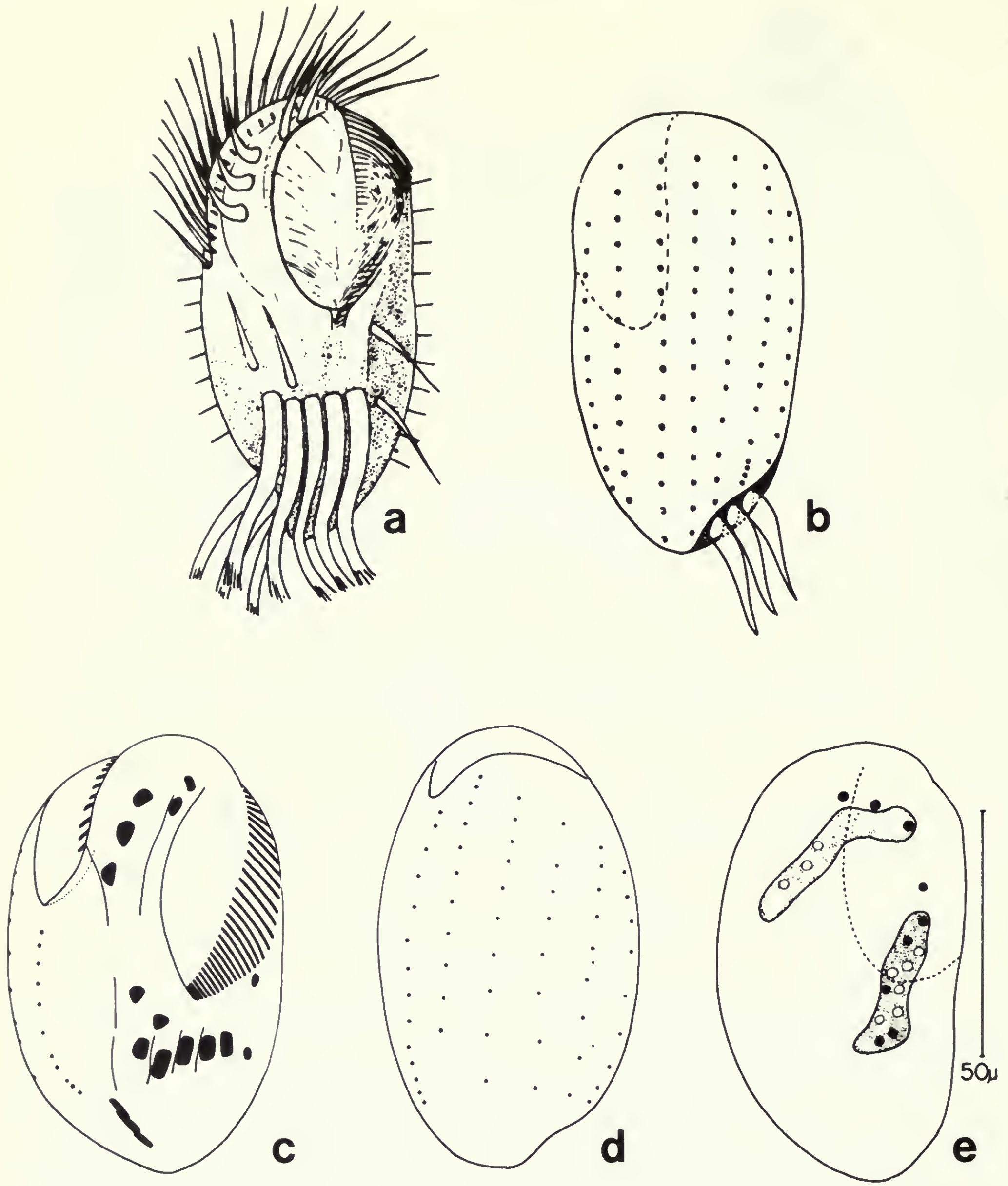

Fig. 18 *Diophrys peloetes*: (a, b) ventral and dorsal surfaces, after Borror, 1963 (called *D. scutum*); (c–e) ventral and dorsal silver-line systems, and nuclei, after Borror, 1965*a*.

Notes. Agamaliev (1967) considered the presence of four right caudal cirri and three macronuclei to be the diagnostic features of this species. The uneven number of macronuclei is rather strange and could perhaps represent an interdivisional state.

Diophrys scutoides Agamaliev, 1967

Description (Fig. 20). *D. scutoides* is 110–120 μm long. The body is oval with a prominent concavity on the posterior right edge. The AZM of 75–80 membranelles borders the left edge of a wide peristome and continues along the anterior edge to extend a third of the body length

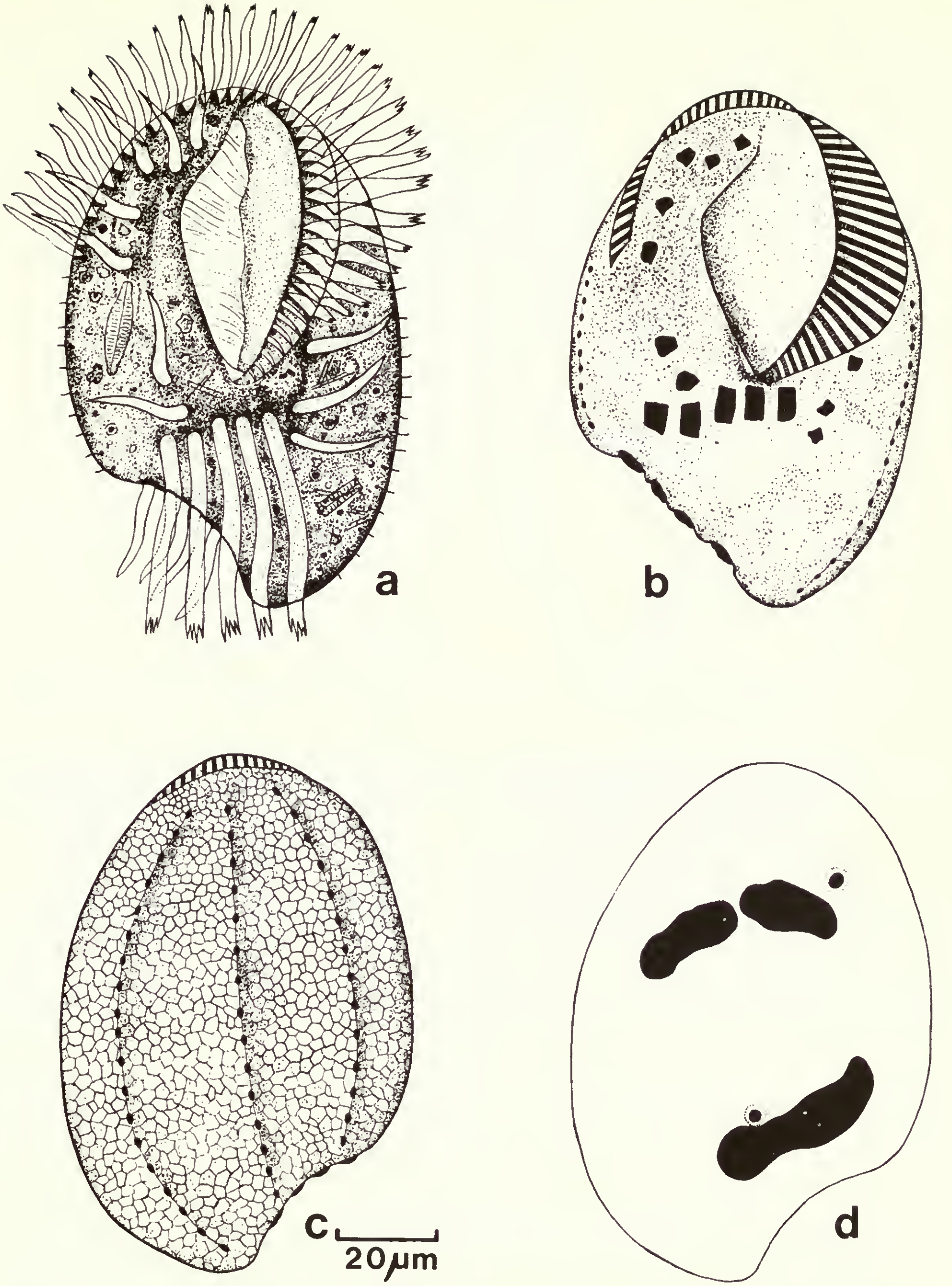

Fig. 19 *Diophrys quadricaudatus*, after Agamaliev, 1967: (a) ventral surface of living cell (b–d) stained ventral surface, dorsal surface and nuclei.

down the right side. There are 3 right caudal, 5 transverse and 2 left marginal cirri but only 5 frontoventral cirri. The two elongate macronuclei are nodular and are accompanied by three micronuclei. The silver-line system consists of 5 dorsolateral kineties with mesh-like dorsal and ventral argyromes.

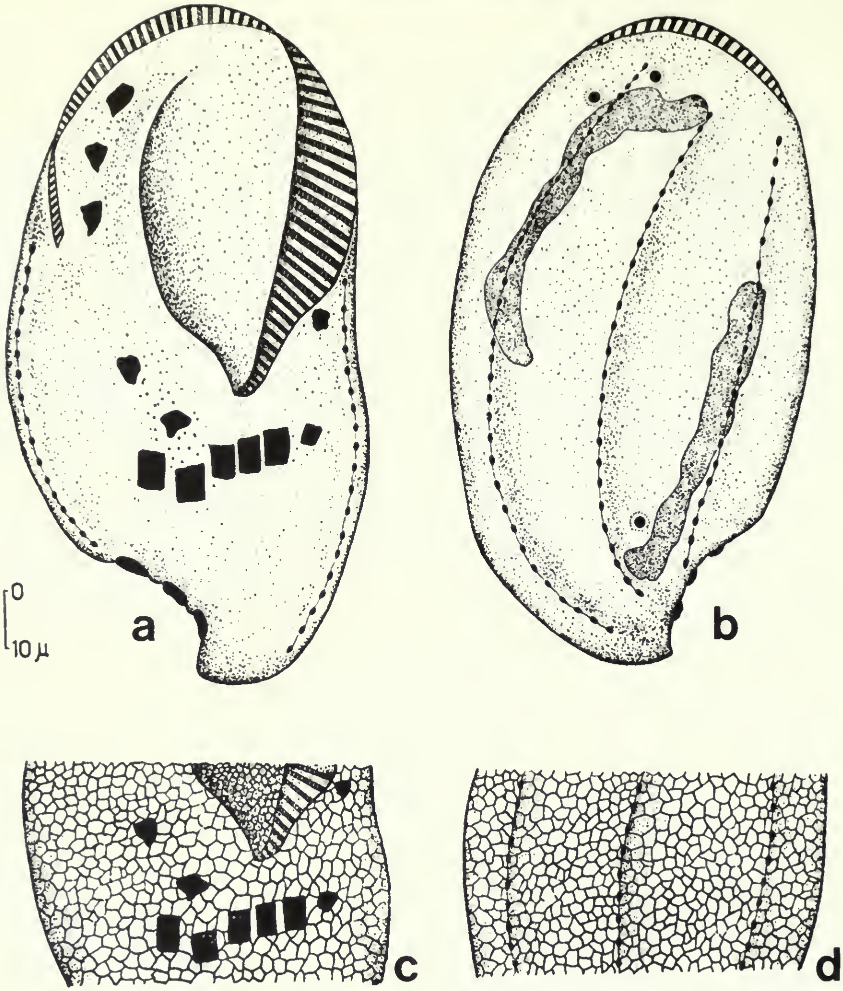

Fig. 20 *Diophrys scutoides*, after Agamaliev, 1967: (a) ventral surface; (b) dorsal surface; (c, d) ventral and dorsal argyromes.

NOTES. Agamaliev (1967) described this species from the Caspian Sea. Apart from being slightly smaller in size, it differs from *D. scutum* in having five instead of seven frontoventral cirri.

Diophrys tetramacronucleata Kattar, 1970

DESCRIPTION (Fig. 21). This is a small (55–65 μm long) species. The body is oval except for the concavity at the posterior right edge. The AZM consists of about 36 membranelles which extend about halfway down the body on the left but hardly at all on the right. There are 7 frontoventral, 5 transverse, 2 left marginal and 3 right caudal cirri. There are 5 dorsolateral kineties and 4 ovoid macronuclei.

NOTES. The original description of this species was brief and only the presence of four macronuclei distinguished it from the type species. Although it is suspected that Kattar (1970) described an interdivisional specimen, it is provisionally included here as a nominal species. Kattar (1970) stated that protargol impregnation showed the presence of three median and two dorsolateral kineties he provided no diagram of these structures. The

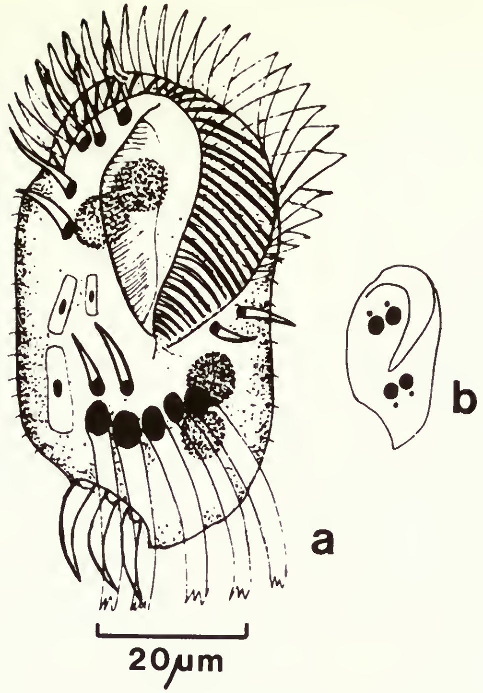

Fig. 21 *Diophrys tetramacronucleata*, after Kattar, 1970: (a) ventral surface; (b) nuclei.

redescription and photographs of this species by Hartwig (1974) are also incomplete although the presence of four macronuclei was clearly demonstrated.

Diophrys multinucleata Hartwig, 1973

Description (Fig. 22). *D. multinucleata* is a medium sized (76–118 µm long) highly thigmotactic species. The body is oval to rectangular in outline with the dorsal surface being arched and the ventral surface flattened. There is a small but distinct projection on the anterior right corner of the body. The peristome is about two-thirds of the body length. The AZM consists of about 30 membranelles lying along the left of the peristome and a few larger membranelles along the anterior edge of the body. The frontoventral cirri are arranged in two distinct groups: the 5–6 large 'frontals' are in the anterior and the two very small 'ventrals' lie close to the transverse cirri. There are 4 long transverse, 3 right caudal and 3 left marginal/caudal cirri. There are at least 20 macronuclei present.

Notes. This species is characterised by the presence of over twenty macronuclei which is unique in the genus, otherwise it is similar to *D. irmgard* in cirral arrangement, particularly in the caudal positioning of the left marginal cirri which Hartwig (1973, 1974) considered to be a feature of diagnostic importance.

Genus *URONYCHIA* Stein, 1859

Introduction

Stein (1859*a*, 1859*b*) established and described the genus *Uronychia* and transferred *Trichoda transfuga* Muller, 1786 to the genus as the type species. Between 1901 and 1928, five new species were described and Kahl (1932) included a key to them in his classical compendium. Since then only one addition, *Uronychia bivalvorum* Fenchel, 1965, has been

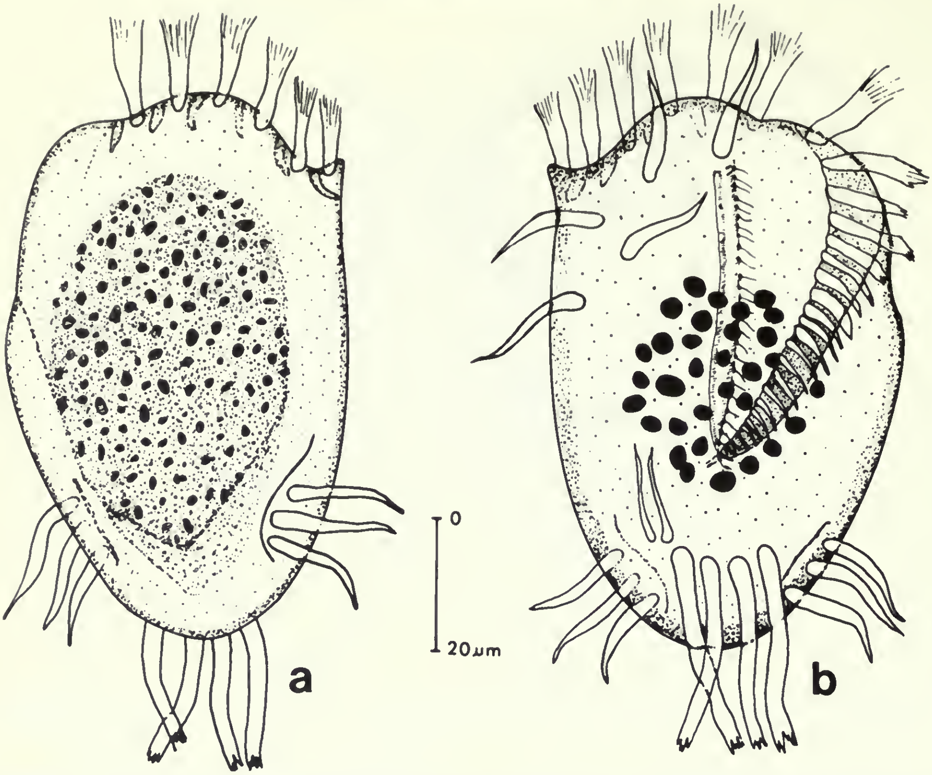

Fig. 22 *Diophrys multinucleata,* after Hartwig, 1973: (a) dorsal surface; (b) ventral surface showing nuclei.

made which he found in the mantle cavity of certain lamellibranch molluscs. *Uronychia* is characterised by its enormous peristome region occupying half of the ventral surface with conspicuous peristomial membranes, the three posterior groups of large cirri, the apparent absence of frontoventral cirri and by its rapid backward motion (Bullington, 1940). However, there are few features which clearly distinguish the described species from one another. Many of the features used in the past are variable so that here only four nominal species are recognised.

(*a*) *Shape.* The typical *Uronychia* body is oval. Dorsal ribs, ridges or striations are often mentioned in descriptions but there are few data on the variability of these structures. Ventrally, there are two large posterior cavities which accommodate the transverse and left marginal cirri. In general, the right caudal cirri of *Uronychia* are attached more dorsally than those in *Diophrys*, so the oval body outline is without the dorsolateral concavity at the posterior right which is characteristic of the latter genus. However, Buddenbrock (1920) described *U. heinrothi* with an 'Ausschnitt' (notch) on the posterior right edge which can make the posterior border S-shaped. Similarly, Taylor (1928) described an 'uncinus' on *U. uncinata* which he stated apparently owes its origin in part to an attenuation of the remnant which holds proter to opisthe during the final stages of division.

It seems likely that the 'Ausschnitt' and 'uncinus' are the same structure and as Buddenbrock (1920) noted that it was variable in extent and absent from some individuals then it cannot be used as a reliable diagnostic character. Indeed if it is formed during division then it could only be present in the proter of a dividing cell.

(*b*) *Size.* The distinctive sizes of *U. magna* and *U. setigera* are here considered to be diagnostically significant. The former at 450 µm long is the largest species so far described in the family Euplotidae, and the latter at 40–50 µm long is the smallest *Uronychia* species. The sizes of the remaining species fall within the range of 70–250 µm long. The size of the type species *U. transfuga* has been noted to vary between 50–150 µm long (Kahl, 1932) but Bullington (1940) separated *U. heinrothi* from *U. transfuga* by the larger size (129–264 µm long) of the species he observed. However, Buddenbrock (1920) described *U. heinrothi* as having the range 70–250 µm in length. It is apparent that the size variation of these two species is great and their ranges overlap. Since there are no other significant distinguishing features, these two species are here regarded as being synonymous.

(*c*) *Adoral Zone of Membranelles.* The ventral surface of *Uronychia* is dominated by an enormous peristome with conspicuous membranelles and membranes. Unlike the rest of the Euplotidae, the AZM of *Uronychia* consists of large membranelles along the anterior of the body and 4–5 smaller paroral membranelles at the posterior left of the peristome and there are undulating membranes along both sides of the peristome. Fenchel (1965) was of the opinion that it was the fusion of the adoral membranelles which forms the membrane along the left peristomial border. These peristomial membranes and membranelles may be observed to be closed over the peristome region or spread out and wing-like. The paroral membranes are often found in a pocket-like invagination of the peristomial wall.

Buddenbrock (1920) described the presence of two large peristomial membranes in *U. heinrothi* but these appear to be split into five parts in one of his diagrams. Bullington (1940) observed four peristomial membranes on his specimens of *U. heinrothi* plus another large membrane close to the posterior right edge of the body. This marginal membrane has been described only on this occasion so it has not been used here as a diagnostic character. Although the peristomial membranes of *U. heinrothi* appear to be larger and more numerous than has been observed in *U. transfuga*, it is not considered to be a reliable character. On the other hand, Calkins (1902) described 'flagella-like' cirri in the peristome of *U. setigera* which have subsequently been noted by other authors (Buddenbrock, 1920; Young, 1922; Kahl, 1932; Kattar, 1970). This feature is apparently distinctive and consistent and is therefore useful in the identification of *U. setigera*.

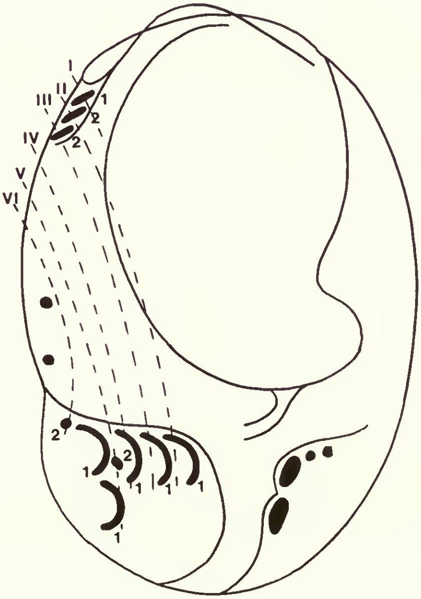

Fig. 23 Arrangement and numbering of cirral streaks in *Uronychia transfuga*, after Wallengren, 1901.

(*d*) *Cirri.* One of the most distinctive generic features of *Uronychia* is the apparent absence of frontoventral cirri. Wallengren (1901) studied cirral morphogenesis in *U. transfuga* and was first to number the cirral streaks (Fig. 23). He found that there was a small residuum of cirral elements I/1, II/2 and III/2 grouped closely together at the anterior right near the adoral membranelles which he described as membranous cirri. Young (1922) noted these in three *Uronychia* species and described them as cirri-like membranelles, but it was Buddenbrock (1920) who illustrated three similar small cirrus-like structures at the anterior left as well as on the right. Wallengren (1901) showed that the cirri V/2 and VI/2 which form the 'ventrals' in *Euplotes* and *Diophrys* lie among the transversals in *U. transfuga* and they appear like 'satellites' in this group of cirri. These cirri have not yet been observed by other authors but Buddenbrock (1920), Young (1922) and Taylor (1928) described the presence of one slender cirrus at the right of the transversals in *U. setigera*, *U. heinrothi* and *U. uncinata*.

All species of *Uronychia* have 4 or 5 transverse cirri. Young (1922) considered the possession of four transversals in *U. binucleata* to be a specific character even though he recorded that the number of transversals in *U. transfuga* varied between 4 and 5. To the left of the ventral cavity from which the transversals emerge, there is another cavity which accommodates the two enormous left marginal cirri with a variable number of small cirri or cilia. The right caudal cirri emerge dorsally on the posterior right and are invariably sickle-shaped. All of the described species have three right caudals except *U. magna* which was shown as having two by Pierantoni (1909), although he also observed only two right caudals in *U. transfuga* which others have shown to possess three. Bullington (1940) discussed the attachment and movement of the right caudal cirri in *Uronychia* (Fig. 24).

In addition to these three groups of large cirri, two small right marginal cirri have been observed in most *Uronychia* species. Fenchel (1965) distinguished *U. bivalvorum* from *U. transfuga* partly by the absence of these two small cirri but it should be noted that both *U. transfuga* and *U. setigera* have also been described without right marginals.

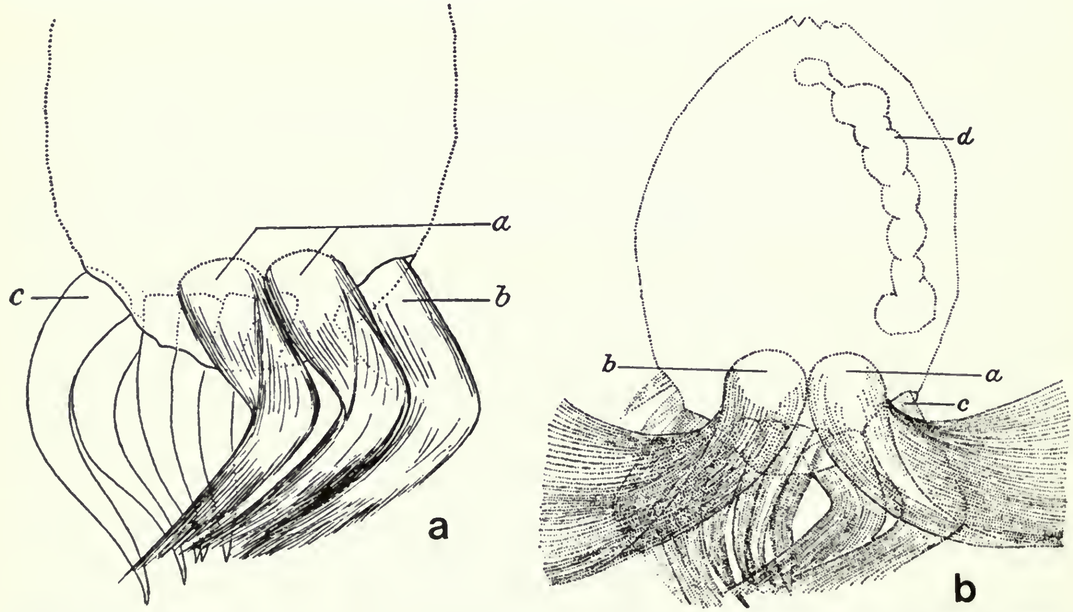

Fig. 24 Arrangement of the right caudal cirri of *Uronychia transfuga*, after Bullington, 1940 (called *U. heinrothi*): (a) showing two large cirri attached in the mid-dorsal region of the posterior body end with a cirrus on the right; (b) showing two defimbriated cirri attached to either side of the mid-line and one cirrus attached in a pocket near the right edge and slightly below the other two cirri.

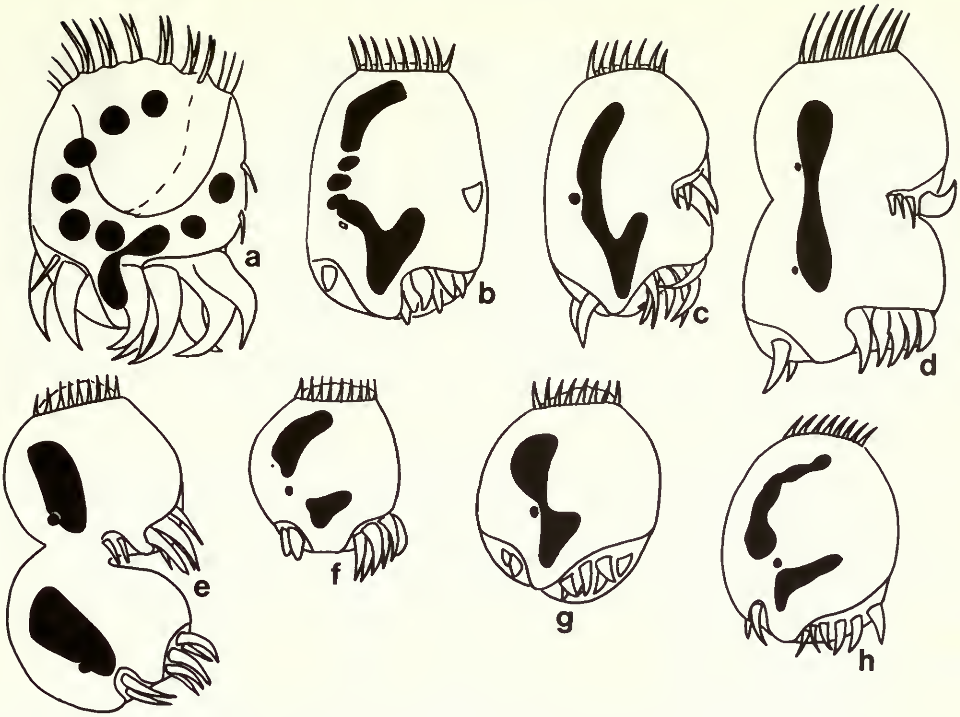

Fig. 25 Stages in cell division of *Uronychia transfuga*, after Calkins, 1911: (a) resting stage; (b) condensation of the macronucleus; (c, d) later stages in division; (e) just before cell separation; (f–h) daughter cells immediately, 15 minutes and 1 hour after separation.

Kahl (1932) noted the presence of a long slender right caudal cirrus in *U. binucleata* which he considered to be of diagnostic value, similarly Young (1922) described such a cirrus in *U. setigera* although no others have reported its presence. It is evident that cirral numbers and arrangements in this genus are highly variable and therefore of little diagnostic importance.

(*e*) *Nuclear features*. Kahl (1932) relied heavily on the nuclear features of *Uronychia* in his key to the species. For example, he stated that *U. transfuga* had, without exception, two sausage-shaped macronuclei with a micronucleus and that *U. magna* and *U. heinrothi* had their nuclei split into many fragments. However, *U. transfuga* had already been seen with its macronucleus in many fragments. Calkins (1911) described the nuclear reorganisation of *U. transfuga* and showed that the macronucleus just after cell division was in two parts but that it was a fragmented C-shape when at the resting stage (Fig. 25). The macronucleus of *U. transfuga* has been described as having a fragmented C-shape, like a string of beads or partially fused, and in two parts (Fig. 26) (Buddenbrock, 1920; Bullington, 1940). Borror (1972) has also noted that the macronuclear shape and number were variable and for this reason considered *U. heinrothi* to be synonymous with the type species.

Calkins (1902) described *U. setigera* with a single ovoid macronucleus but Young (1922) observed two irregular macronuclei in his specimens of the same species. Fenchel (1965) distinguished *U. bivalvorum* from the type species partly on the basis of its nucleus which he described as ‘an irregular structure divided into two or more parts of unequal size’: this would lie within the range of variability already noted above for *U. transfuga.* Kattar (1970) distinguished between *U. transfuga* and *U. setigera* by their possession of 9–15 and 2 nodular macronuclei respectively, although he also concluded that the six species recognised by Kahl (1932) including *U. setigera* could be varieties of *U. transfuga*. Although the number and shape of the macronuclei in *Uronychia* appear to be highly variable this is not the case with

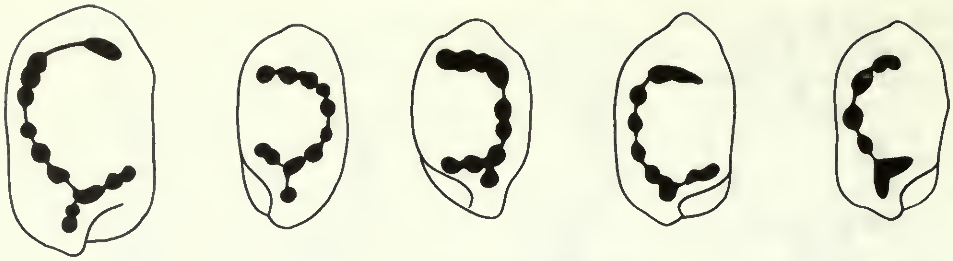

Fig. 26 Nuclear variation in *Uronychia transfuga*, after Buddenbrock, 1920 (called *U. heinrothi*).

the micronucleus. Most species possess a single micronucleus but *U. binucleata* is characterised by the presence of two micronuclei. Only one other species, *U. magna*, has been recorded with two micronuclei.

(*f*) *Dorsal silver-line system.* Kattar (1970) noted the presence of four kineties on the dorsal surface of *U. transfuga* and five on *U. setigera*, while Reiff (1968) illustrated five dorsolateral kineties on the former species. The kineties which have only recently been described appear to correspond in number and position with the dorsal ridges and striations that are sometimes described by earlier authors. However, far more data are required before the diagnostic importance of the silver-line systems of *Uronychia* can be assessed.

Diagnosis of *Uronychia*

Marine hypotrichs of variable size, mostly within the range 50–250 μm long, but up to 450 μm long. Body oval and smooth in outline, dorsal surface smooth or with ridges. Peristome large with conspicuous membranes. The AZM is limited to the anterior border and the paroral region. There are 4–5 transverse and 2 left marginal cirri which emerge from prominent ventral cavities. The 3 large right caudal cirri are attached to the dorsal surface and there are sometimes 2 right marginal cirri present. The frontoventral cirri are reduced to a field of 3 near the origin of the AZM. The macronuclei are variable in number and shape and there are 1 or 2 micronuclei. Characteristically moves backwards rapidly.

Key to the species of *Uronychia*

1	50–250 μm long	2
	Smaller than 50 μm long or larger than 250 μm long	4
2	With a single micronucleus	3
	With two micronuclei	5
3	Peristomial cirri present	***U. setigera***
	Peristomial cirri absent	***U. transfuga***
4	40–50 μm long	***U. setigera***
	About 450 μm long	***U. magna***
5	About 450 μm long, macronucleus moniliform and C-shaped	***U. magna***
	60–80 μm long, macronucleus in 3–5 pieces	***U. binucleata***

Species descriptions

Uronychia transfuga (Muller, 1786) Stein, 1859

Trichoda transfuga Muller, 1786
Ploesconia scutum Dujardin, 1841 (in part)
Campylopus paradoxus Claparède & Lachmann, 1858
Uronychia heinrothi Buddenbrock, 1920
Uronychia uncinata Taylor, 1928
Uronychia bivalvorum Fenchel, 1965

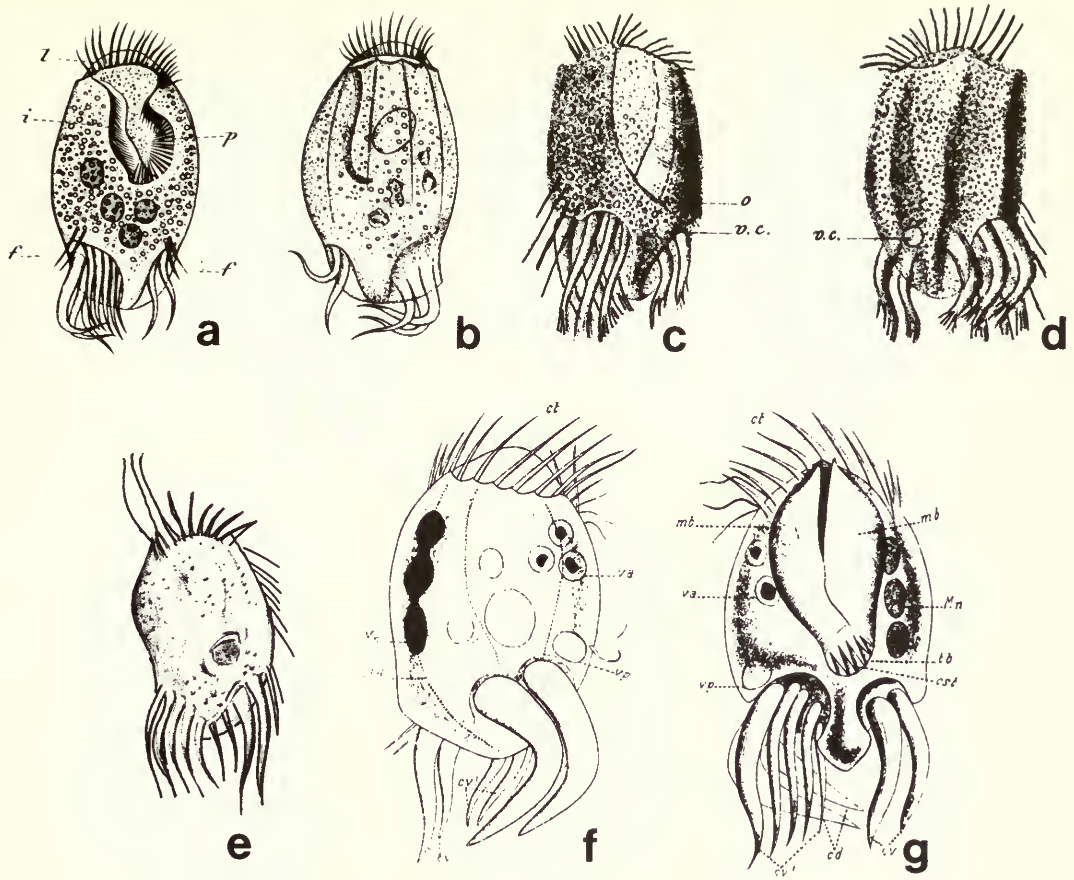
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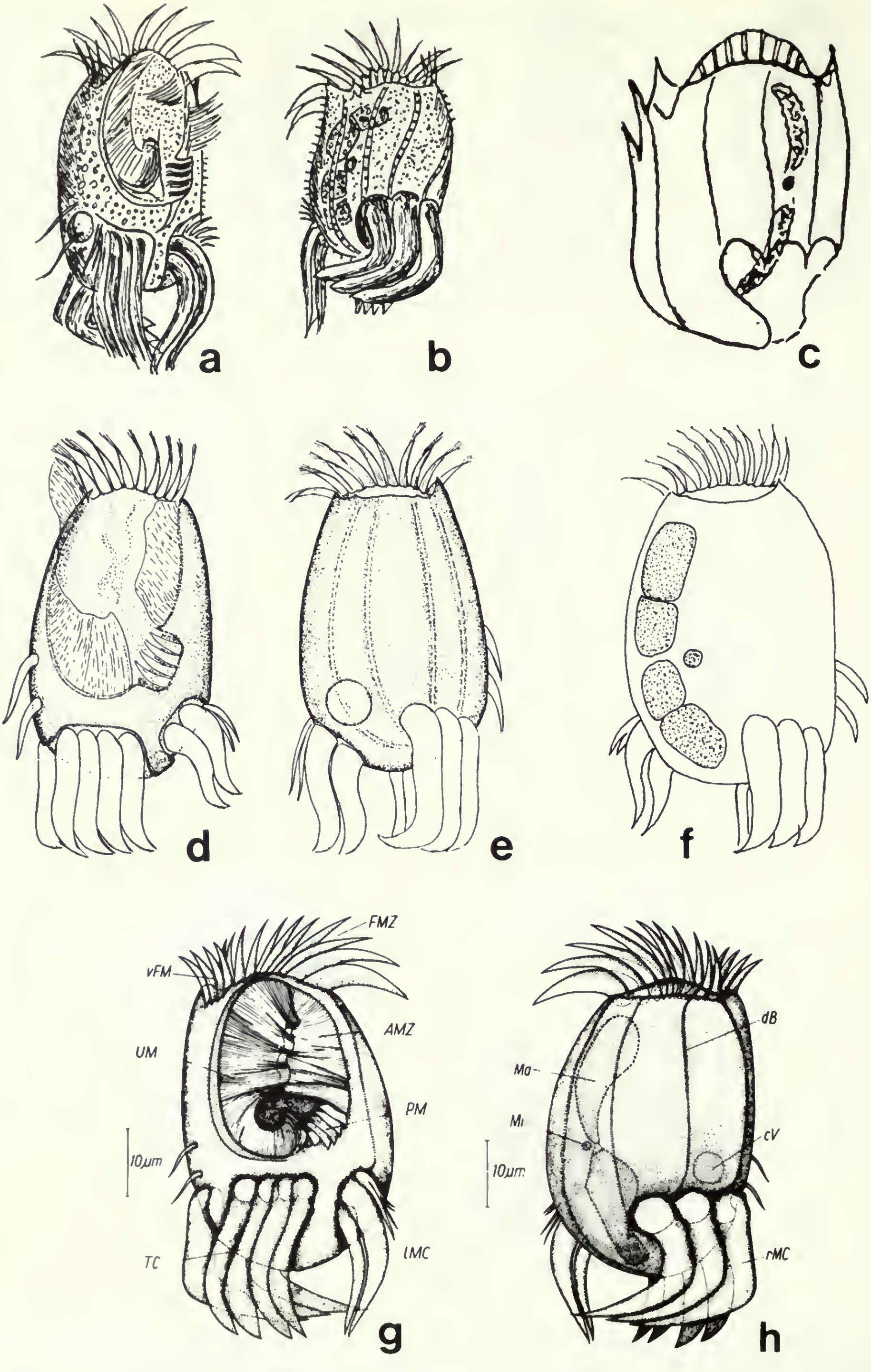
Fig. 27 *Uronychia transfuga*: (a, b) ventral and dorsal surfaces, after Stein, 1859*a*; (c, d) ventral and dorsal surfaces, after Claparède & Lachmann, 1858 (called *Campylopus paradoxus*); (e) dorsal surface, after Dujardin, 1841 (called *Ploesconia scutum*); (f, g) ventral and dorsal surfaces showing nuclei, after Pierantoni, 1909; (h) ventral surface and nuclei, after Calkins, 1911; (i) dorsal surfaces and nuclei, after Young, 1922.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TC
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dB
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rMC
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Fig. 28 *Uronychia transfuga*: (a–c) ventral and dorsal surfaces showing nuclei, after Kahl, 1932 (c called *U. uncinata*); (d–f) ventral and dorsal surfaces and nuclei, after Fenchel, 1965 (called *U. bivalvorum*); (g, h) ventral surface and dorsal surfaces showing nuclei, after Reiff, 1968.

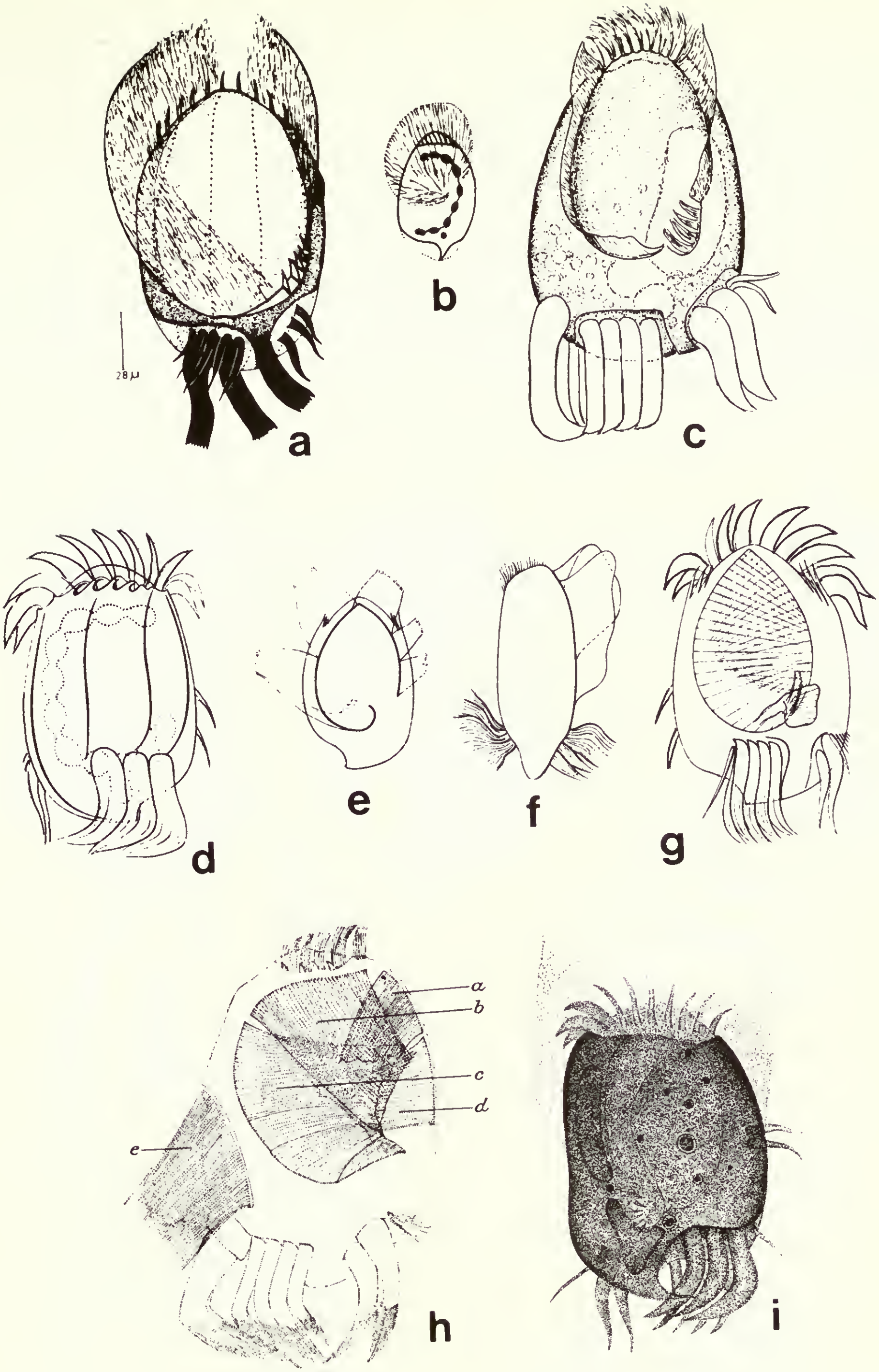

Fig. 29 *Uronychia transfuga*: (a, b) ventral surface and nuclei, after Kattar, 1970; (c) ventral surface, after Fenchel, 1965 (called *U. bivalvorum*); (d–g) ventral surface, dorsal surface showing nucleus, ventral view and lateral view of peristomial membranes, after Buddenbrock, 1920 (called *U. heinrothi*); (h) ventral surface, after Bullington, 1940 (called *U. heinrothi*); (i) dorsal surface, after Taylor, 1928 (called *U. uncinata*).

DESCRIPTION (Figs 27, 28 & 29). This is a cosmopolitan species. The oval shaped body is variable in size (50–260 μm long), its dorsal surface is arched and may be smooth or with 3–4 ridges. At the posterior right there are the 3 characteristically sickle-shaped right caudal cirri. The large peristome and two posterior cavities occupy most of the ventral surface. Prominent adoral membranelles are situated along the anterior edge of the body and these emerge dorsally. At the posterior left of the peristome, there are 4–5 paroral membranelles lying in a pocket-like invagination. Large undulating membranes border two sides of the peristome. There are 4–5 large transverse cirri implanted in the larger posterior cavity on the right, sometimes with 1 or 2 satellite cirri. In the posterior left cavity there are 2 large marginal cirri sometimes accompanied by a few, usually 2, small cirri or cilia. The macronucleus varies from being a moniliform (5–13 segments) C-shape at resting stage, to being 2 irregular masses immediately after cell division. The silver-line system consists of 3–5 dorsolateral kineties. It has been observed in the mantle cavities of the lamellibranch molluscs *Thyasira flexuosa* and *T. sarsi*.

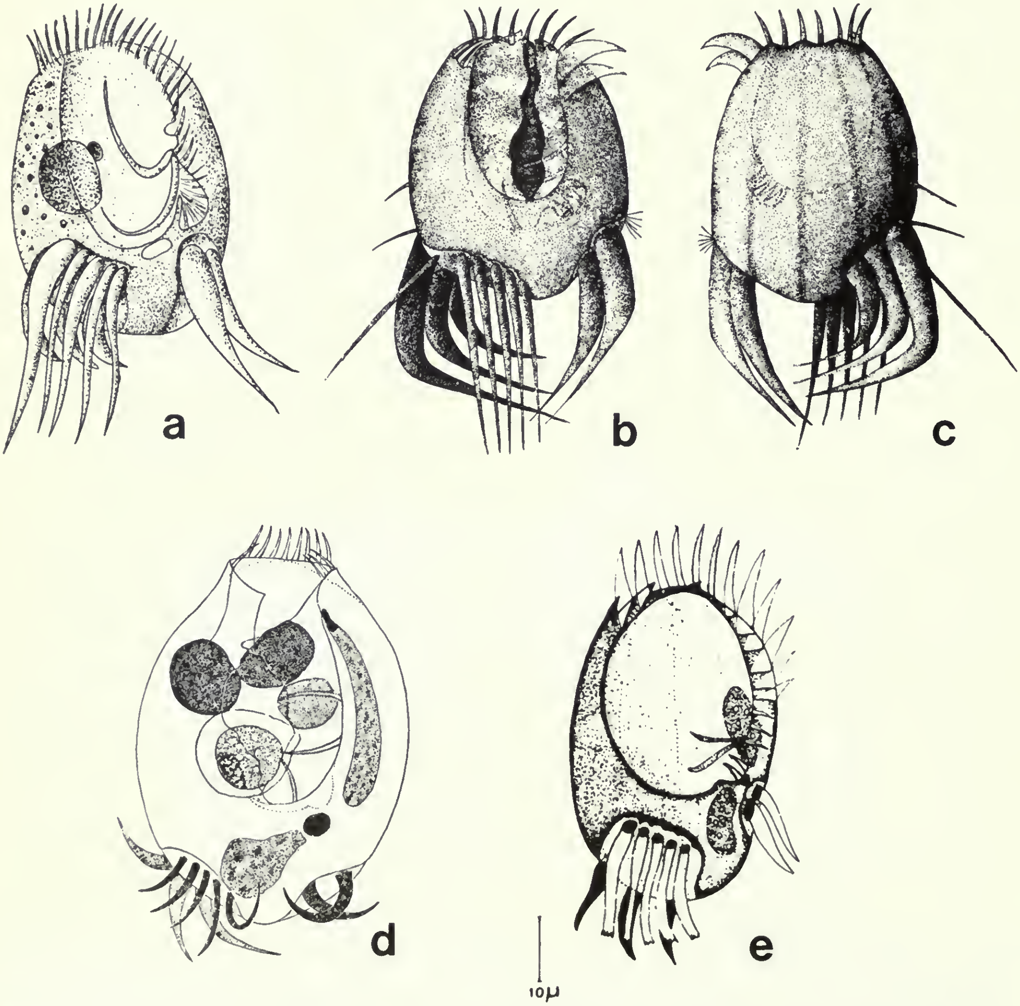

Fig. 30 *Uronychia setigera*: (a) after Calkins, 1902; (b–d) after Young, 1922; (e) after Kattar, 1970.

Notes. Stein (1859*a*, *b*) established the genus *Uronychia* and redescribed *U.* (*Trichoda*) *transfuga* Muller as the type species. *U. transfuga* has since been identified by many workers from various localities (see Hartwig 1973, 1974). As discussed earlier *U. heinrothi*, *U. uncinata* and *U. bivalvorum* were established on characters that are now known to be variable and unreliable. These three species are here regarded as synonyms of the type species until more convincing data become available.

Uronychia setigera Calkins, 1902

Description (Fig. 30). This is the smallest (40–50 µm long) species yet described. The dorsal surface is arched and is sculptured longitudinally by 3–4 ridges. There are 2–3 flagella-like cirri in the large peristome and there are about 4 paroral membranelles. Wide undulating membranes lie on each side of the peristome. There are 3 curved right caudal cirri attached dorsally and a long thin satellite cirrus has been observed. In the two ventral cavities there are 4–5 transverse cirri and 2 large left marginal cirri. The macronucleus is usually in 2 band-like parts with a micronucleus between them but a single spherical macronucleus has also been observed in this species. There are 5 dorsolateral kineties.

Notes. This species is characterised by the presence of flagella-like cirri extending from the posterior left margin into the peristome (Calkins, 1902). This author further distinguished it from the type species by its single ovoid macronucleus; however later authors (Young, 1922; Kattar, 1970) reported two macronuclei. Kattar (1970) impregnated the cell with protargol but failed to clearly illustrate the silver-line system.

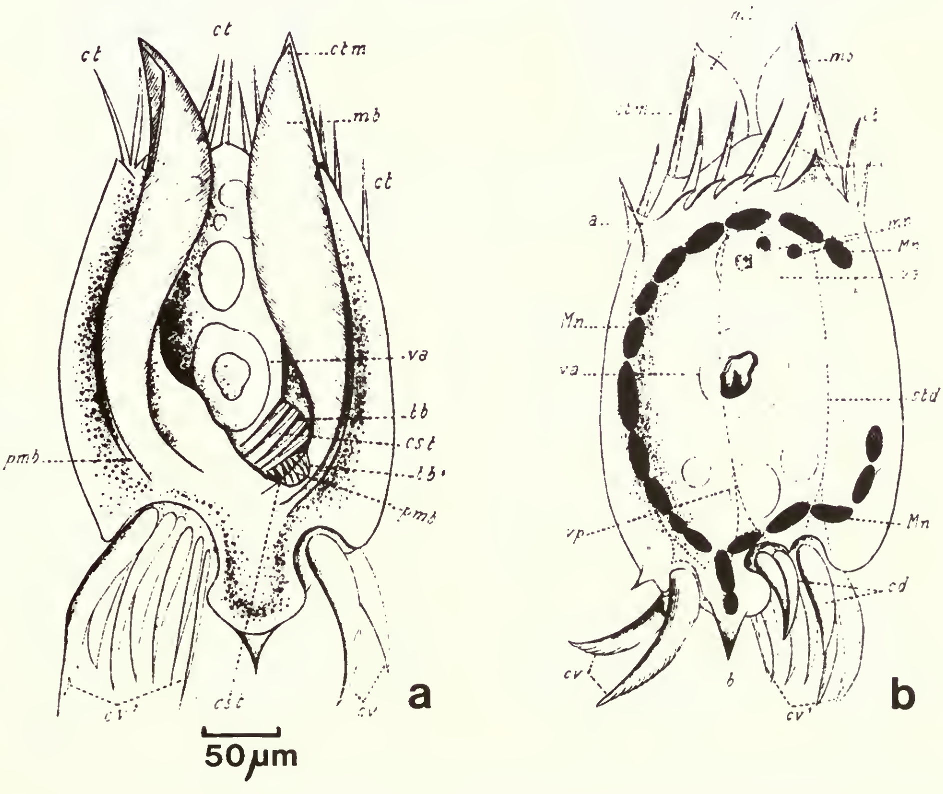

Fig. 31 *Uronychia magna*, after Pierantoni, 1909; (a) ventral surface; (b) dorsal surface.

Uronychia magna Pierantoni, 1909

DESCRIPTION (Fig. 31). This is the largest species yet recorded (450 µm long). The body shape is approximately oval in outline but is ornamented at either end. The anterior dorsal edge is serrated and there are two short spines on the posterior left dorsal border. The dorsal surface is longitudinally striated. The peristome is extensive, occupying most of the ventral surface. The AZM is located anteriorly in a posterior pocket in the peristome. There are two large undulating membranes, one on each side of the peristome. There are 6 transverse, 2 left marginal and 3 right caudal cirri. The macronucleus is in many pieces forming a string of beads which follow the curve of the left side of the body so that it is C-shaped. Anteriorly there are 2 micronuclei.

NOTE. This species has apparently been described on a single occasion.

Uronychia binucleata Young, 1922

DESCRIPTION (Fig. 32). *Uronychia binucleata* is 60–80 µm long. The dorsal surface is arched

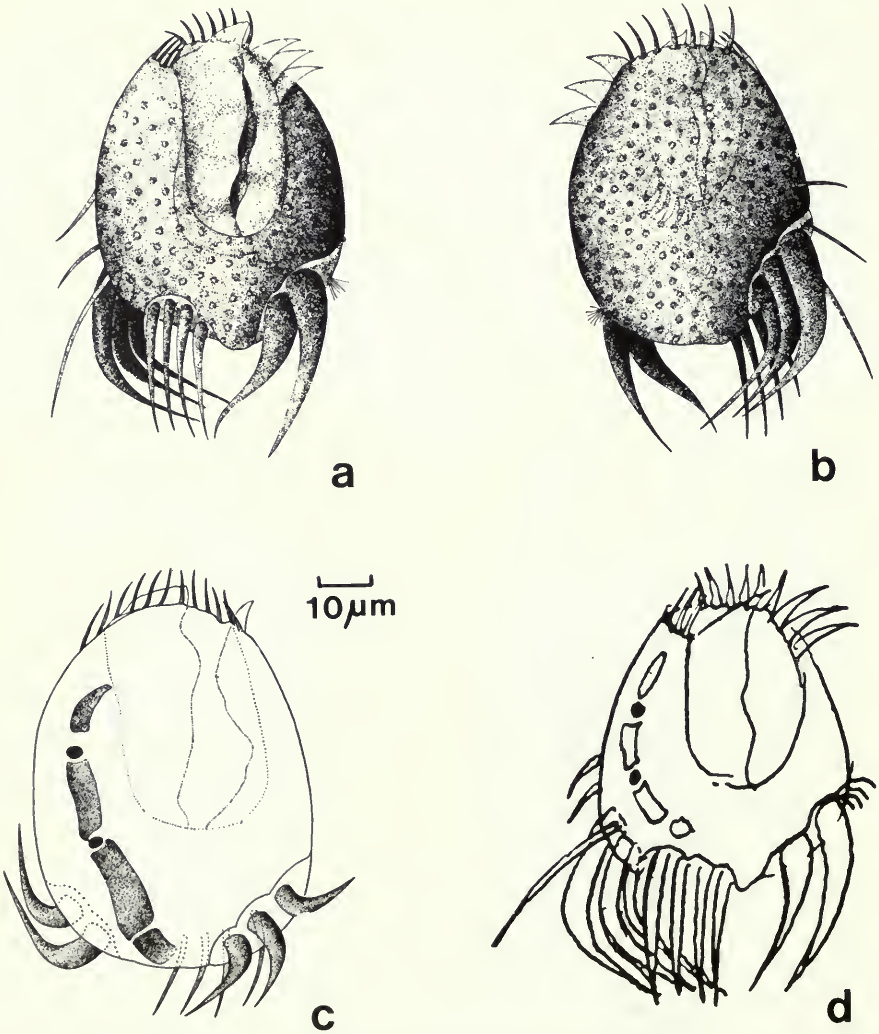

Fig. 32 *Uronychia binucleata*: (a–c) ventral surface, dorsal surface and nuclear features, after Young, 1922; (d) after Kahl, 1932.

and decorated with many small pits. The peristome is bordered on either side by a large undulating membrane and at the anterior left there are 3 delicate sickle-shaped membranelles. About 4 paroral membranelles lie in the 'buccal' pocket. There is a long slender cirrus accompanying the 3 curved right caudal cirri, 4 transverse, 2 left marginal and 2 right marginal cirri. The macronucleus is in 3–5 fragments and 2 micronuclei.

NOTES. Young (1922) established this species which he showed to be almost identical to *U. setigera* in his comparative study. He distinguished his species by the absence of peristomial cirri, the presence of 4 or less transverse cirri, and the presence of a slender right caudal cirrus in addition to the two micronuclei. Although Young (1922) described a satellite cirrus in *U. setigera* which he considered to be significant, curiously he failed to mention it in *U. binucleata* even though he illustrated it. Here the presence of two micronuclei is used to characterise the species: should future studies show that the number of micronuclei to be variable, then it would become synonymous with *U. transfuga*.

Genus *CERTESIA* Fabre-Domergue, 1885

Introduction

Fabre-Domergue (1885) described an organism that was very similar to *Euplotes* except that it had a row of left marginal cirri, no caudal cirri and the macronucleus was in four parts. In his view this was sufficient to create the new genus *Certesia* although later both Bütschli (1889) and Sauerbrey (1928) considered it to be a subgenus of *Euplotes*. Since the description of the type species, *Certesia quadrinucleata* Fabre-Domergue, 1885, only one other species, *Certesia ovata* Vacelet, 1960, has been described. Vacelet (1960) distinguished it from the type species on account of its smaller size, its more oval shape and its two curved left transverse cirri. Here, these differences are not considered to be sufficient to treat *C. ovata* as a separate species.

Diagnosis of *Certesia*

Oval marine hypotrichs with an anterior nose-like projection on the right anterior body edge. There is a conspicuous AZM which extends a third to halfway down the left side of the body. There are 11–13 frontoventral, 5 large transverse, and a variable number (6–11) of left marginal cirri. There are no caudal cirri. Macronucleus in several parts. Single species genus.

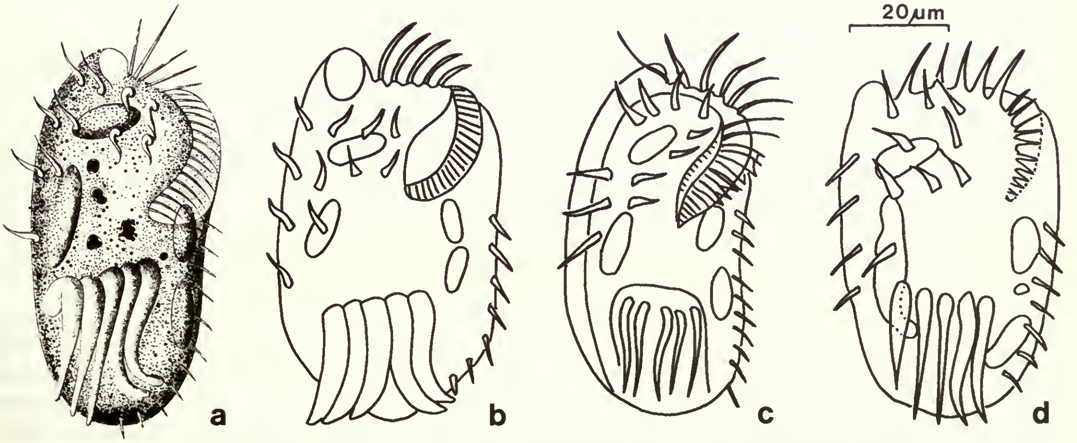

Fig. 33 *Certesia quadrinucleata*: (a) after Fabre-Domergue, 1885; (b) after Sauerbrey, 1928; (c) after Kahl, 1932; (d, e) after Vacelet, 1960 (called *C. ovata*).

Species description

Certesia quadrinucleata Fabre-Domergue, 1885

Certesia ovata Vacelet, 1960

Description (Fig. 33). *Certesia quadrinucleata* is a medium sized (75–80 µm long), oval, rigid and colourless marine hypotrich. The dorsal surface is arched and smooth: the ventral surface flat. The right body border is convex and the left may be slightly concave. There is a distinct nose-like projection on the right of the extreme anterior body edge. The peristome is a third to a half of the body length. The AZM consists of about 5 large membranelles along the anterior border and 15–20 smaller ones along the left edge of the peristome. There are 11–13 frontoventral cirri, 5 large transverse cirri, a row of 6–11 left marginal cirri but no caudal cirri. Four ovoid macronuclei are located in pairs, one pair on the right anterior and one pair on the left below the AZM.

Genus ***GASTROCIRRHUS*** Lepsi, 1928

Introduction

Lepsi (1928) created the genus *Gastrocirrhus* and stated that the type species *Gastrocirrhus intermedius* Lepsi, 1928 possessed characters that were intermediate between the oligotrichs and the hypotrichs. The organism had ventral cirri arranged in groups like those of hypotrichs, but its large anterior funnel-shaped peristome and spiral AZM were more like those of oligotrich genera such as *Stentor*. Kahl (1932) thought that the organism was probably a piece of a fragmented *Oxytricha*, but soon after Bullington (1940) established another species *Gastrocirrhus stentoreus* Bullington, 1940. This has been followed by several other species descriptions.

The six cirri along the right side of *G. intermedius* are here interpreted to be frontoventrals and the remaining ten cirri are called caudals. Bullington (1940) recorded the presence of four marginals, four ventral and two oral/anterior cirri on *G. stentoreus*. These are considered to be frontoventral cirri so that this species may be diagnosed by the presence of only five caudal cirri. In *Gastrocirrhus adhaerens* Fauré-Fremiet, 1954, there are 16 cirri arranged in two rows on the right of the peristome, and 12 in a semi-circle at the posterior. Here, these are interpreted to be frontoventral and caudal cirri respectively. *Gastrocirrhus trichocystus* Ito, 1958 has 18 frontoventral and 13 caudal cirri arranged similarly to those in *G. adhaerens* but the species is characterised by the presence of zones of trichocysts (mucocysts?) on the dorsal and ventral surfaces.

Fauré-Fremiet (1961) created the family Gastrocirrhidae and included the single species genus *Cirrhogaster* Ozaki & Yagui, 1942 in the family. The type species, *Cirrhogaster monilifer* Ozaki & Yagui, 1942 is similar to *G. adhaerens*, but the former species has 10 rather than 16 frontoventral cirri. Dragesco (1965) suggested that these two species were synonymous but here, although *C. monilifer* is considered to be a species of *Gastrocirrhus* it is not considered to be a synonym of *G. adhaerens.*

Diagnosis of *Gastrocirrhus*

Marine hypotrichs that may be dorsoventrally flattened or cup-shaped. There is a large anterior funnel-shaped peristome which opens both anteriorly and ventrally. A well developed AZM borders the C-shaped anterior body edge and winds anti-clockwise down the left of the peristome. There are 5–18 frontoventral cirri, usually arranged in two oblique rows on the right of the peristome: 5–13 caudal cirri along the posterior pole of the body which in some species curve forwards ventrally on the left to give the appearance of transverse cirri. Macronucleus may be oval or moniliform in 11–15 pieces.

Key to the species of *Gastrocirrhus*

1	With 10 frontoventral cirri	4
	With 6, or more than 10 frontoventral cirri	2
2	With 6 frontoventral cirri	***G. intermedius***
	With more than 10 frontoventral cirri	3
3	With 16 frontoventral cirri and 12 thigmotactic caudal cirri, without 'trichocyst' zones	***G. adhaerens***
	With 18 frontoventral cirri, 13 caudal cirri and with dorsal and ventral zones of 'trichocysts'	***G. trichocystus***
4	With 5 caudal cirri	***G. stentoreus***
	With 12–13 caudal cirri	***G. monilifer***

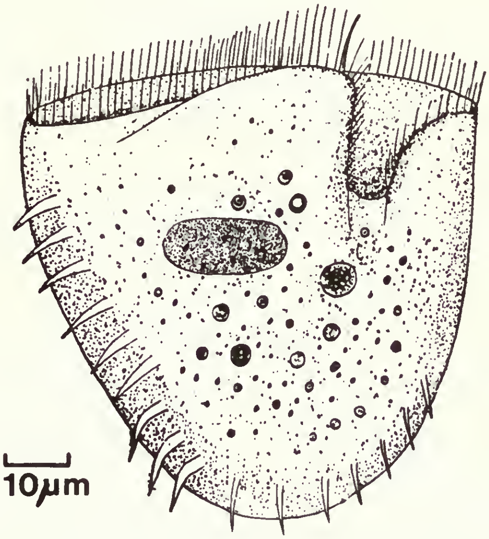

Fig. 34 *Gastrocirrhus intermedius*, after Lepşi, 1928.

Species descriptions

Gastrocirrhus intermedius Lepsi, 1928

Description (Fig. 34). This species is a dorsoventrally flattened cup-shape, approximately 70 µm long. The well developed AZM borders the anterior funnel-shaped peristome. There are 16 cirri in three distinct groups. Near the right body margin there are 6 frontoventral cirri. The caudals are situated along the posterior pole, comprised of a group of 3 sickle-shaped cirri, rather like the right caudal cirri in *Diophrys*, and 7 others to their left which are smaller and straighter. The macronucleus is oval.

Notes. There is only a single description of this, the type species of the genus. The observations of Lepsi (1928) appear to have been made exclusively on living specimens. The arrangement of the cirri and nuclear features do not appear to be as typical as those of the species described later.

Gastrocirrhus stentoreus Bullington, 1940

Description (Fig. 35). *Gastrocirrhus stentoreus* is a medium sized (100 µm long, 70–80 µm wide) perfectly cup-shaped species. The large funnel-shaped peristome has a ventral, elongate opening about two-thirds of the body length and is bordered by a prominent AZM. There are 11 frontoventral cirri on the right of the peristome in groups of two, four and five cirri. At the posterior right margin, there are 5 sickle-shaped caudal cirri.

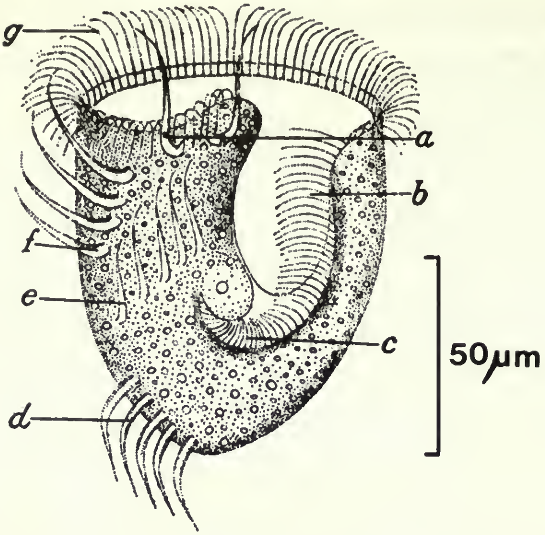

Fig. 35 *Gastrocirrhus stentoreus*, after Bullington, 1940.

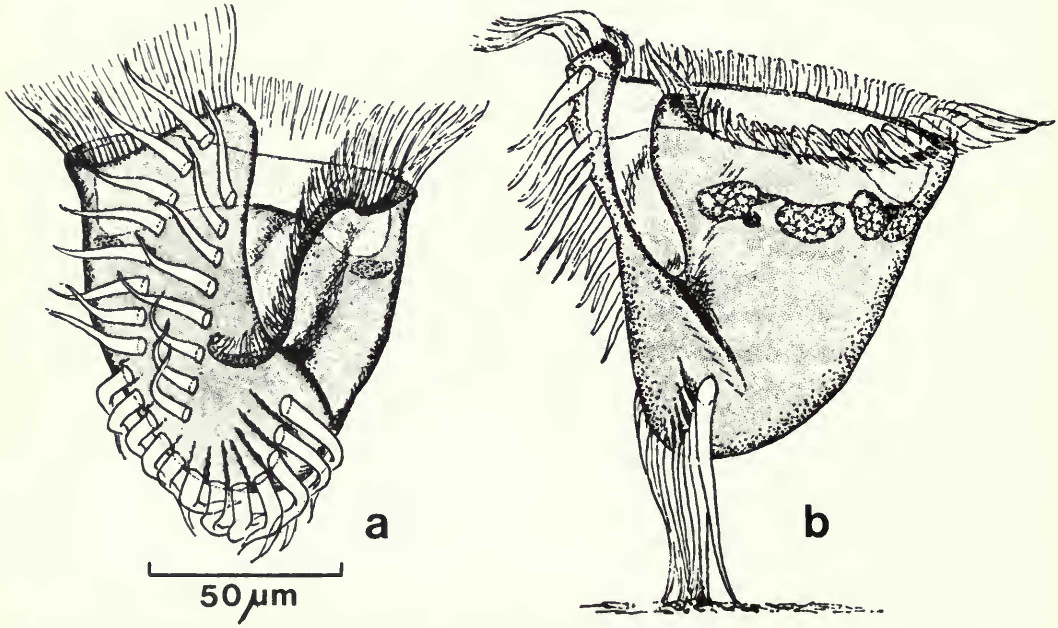

Fig. 36 *Gastrocirrhus adhaerens*: (a) ventral surface; (b) attached to substratum showing nuclei. Both after Fauré-Fremiet, 1954.

Gastrocirrhus adhaerens Fauré-Fremiet, 1954

Description (Fig. 36). This is a medium sized (100 µm long), typically cup-shaped species. The peristome diameter is slightly less than the body length. The AZM, which winds around the anterior of the cell and down the left side of the peristome, consists of about 150 membranelles. The species is characterised by its 12 very long thigmotactic caudal cirri along the posterior border of the cell which can be retracted when not attached to a substratum. There are 16 frontoventral cirri arranged in two rows of 8 cirri on the right of the peristome. The moniliform macronucleus is composed of about 12 pieces: 3–5 micronuclei have been observed.

Gastrocirrhus monilifer n. comb.

Cirrhogaster monilifer Ozaki & Yagui, 1942

Description (Fig. 37). *Gastrocirrhus monilifer* is 95–105 µm long, 75–90 µm wide and cup-shaped. The ventral opening into the large funnel-shaped peristome is about a half the body length. The 10 frontoventral cirri, arranged in two rows, are restricted to the small area on the right of the peristome. There are 12 long caudal cirri. The moniliform macronucleus consists of 11–15 pieces and there are 8 micronuclei scattered along its length.

Notes. Dragesco (1965) suggested that this species should be a synonym of *G. adhaerens*. Here it is considered to be a separate species until further information concerning the variability in numbers of frontoventral cirri become available.

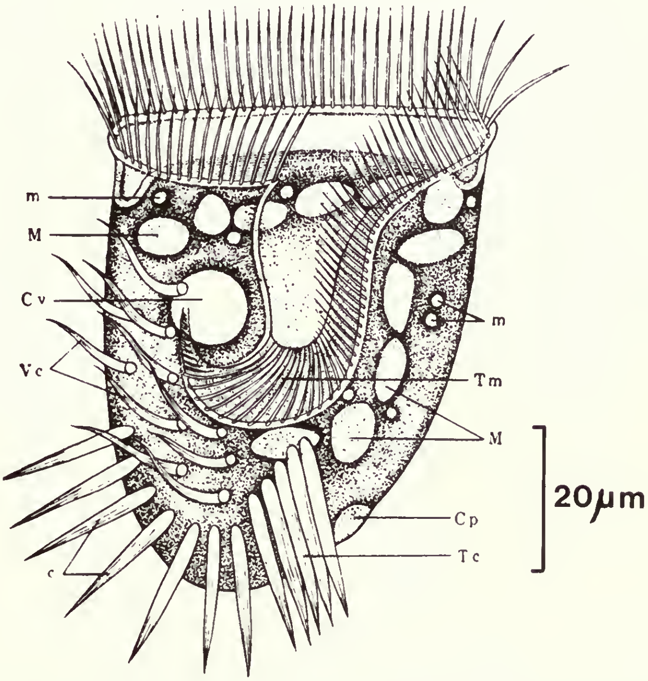

Fig. 37 *Gastrocirrhus monilifer*, after Ozaki & Yagui, 1942 (called *Cirrhogaster monilifer*).

Gastrocirrhus trichcystus Ito, 1958

Description (Fig. 38). *Gastrocirrhus trichocystus* is 90–103 µm long, 82–90 µm wide and cup-shaped. The ventral surface becomes flattened when starved. The large peristome is bordered by numerous long adoral membranelles. There are 18 frontoventral and 13 caudal cirri separated by longitudinal ridges on the ventral surface. The sickle-shaped macronucleus is moniliform with 10–12 pieces. There are usually 8 micronuclei. The species is characterised by bands of 'trichocysts' (mucocysts?) along the anterior and right margin of the dorsal surface, also they are found along the left margin and at the anterior right on the ventral surface.

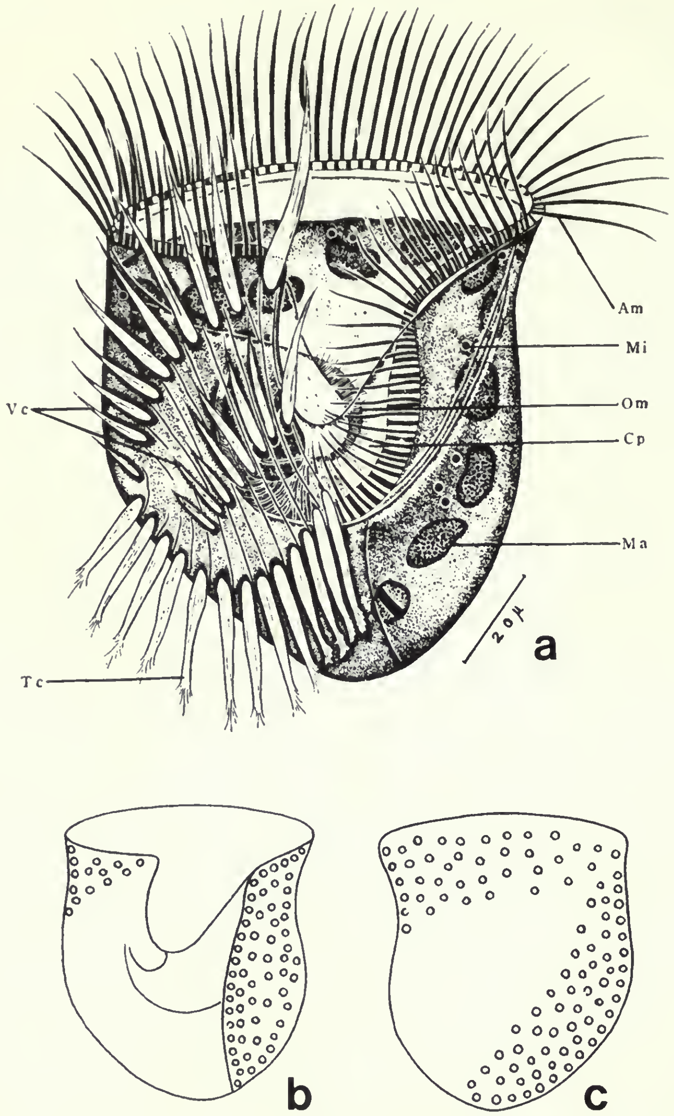

Fig. 38 *Gastrocirrhus trichocystus*, after Ito, 1958: (a) ventral surface; (b, c) ventral and dorsal surfaces showing trichocyst distribution.

Genus *EUPLOTASPIS* Chatton & Séguéla, 1936

Introduction

Chatton & Séguéla (1936) described a *Euplotes*-like hypotrich found in the branchial cavity of the sea squirt, *Ciona intestinalis*. They noted that the organisms were never observed on or around their host and they did not survive without their host for more than 36 hours in a medium which had been used successfully for the culture of many marine *Euplotes*.

This species was found to have many characters similar to those of *Euplotes* but Chatton & Séguéla (1936) noted that its body shape and very thick short cirri were more like those of *Aspidisca*. Furthermore, the AZM was entirely ventral so that it did not border the anterior dorsal surface as in *Euplotes*, and four of the frontoventral cirri were split into two parts which is a distinctive feature. Corliss (1961) placed this genus along with *Paraeuplotes* in the family Paraeuplotidae but later (Corliss, 1977) he transferred it to the family Aspidiscidae.

Diagnosis of *Euplotaspis*

Marine oval hypotrichs living in sea squirts. There is a prominent AZM restricted to the ventral surface. There are 9 frontoventral, 5 transverse and 3–4 caudal cirri. The four frontoventral cirri towards the right body border are split longitudinally into two parts. Macronucleus C-shaped. The dorsal argyrome is like that of *Euplotes vannus* (see Curds, 1975).

Species description

Euplotaspis cionaecola Chatton & Séguéla, 1936

DESCRIPTION (Fig. 39). *Euplotaspis cionaecola* is a 60–70 µm long marine hypotrich found in

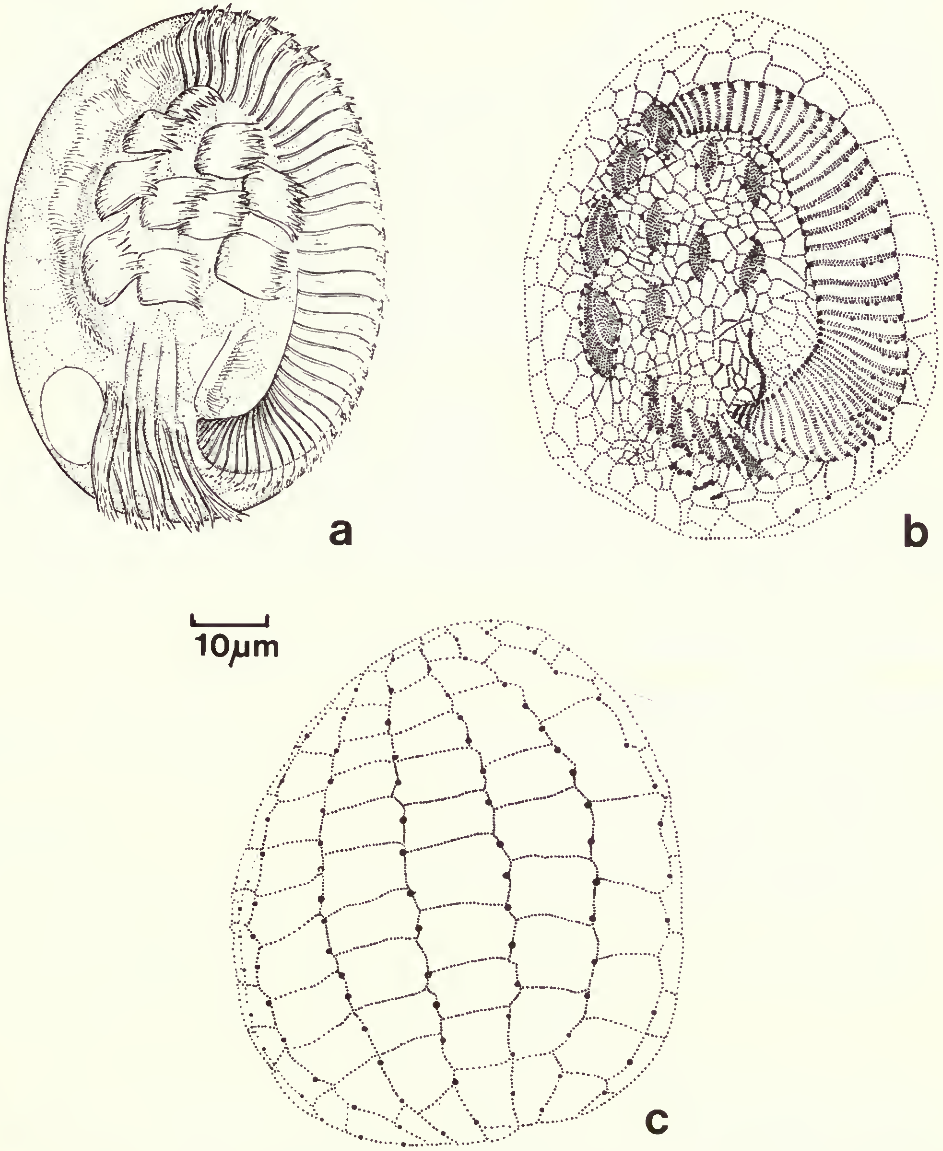

Fig. 39 *Euplotaspis cionaecola*, after Chatton & Séguéla, 1936: (a) ventral surface of living cell; (b, c) ventral and dorsal surfaces of silver-impregnated specimens.

the branchial cavity of *Ciona intestinalis*. The body outline is perfectly oval, convex dorsally and flattened or slightly concave ventrally. The AZM of about 50 membranelles, is a prominent band parallel to, and at a short distance from, the left body margin. There are 10 short, wide frontoventral cirri: the four on the right being split longitudinally. The 5 transverse cirri are separated by marked ridges on the ventral surface. The 3–4 caudal cirri are small and indistinct *in vivo* but can be seen in silver impregnated specimens. The dorsal silver-line system consists of 7–8 dorsal kineties, each carrying about 15 cilia, with simple cross-links between the kineties. The macronucleus is C-shaped and a single micronucleus has been observed at its posterior left.

Genus ***EUPLOTIDIUM*** Noland, 1937

Introduction

Noland (1937) described a hypotrich found in sponges from the Gulf of Mexico and stated that 'the organism differs from *Euplotes*, its nearest relative, in the absence of caudal cirri, and in the more cylindrical shape of the body'. Consequently, he erected the genus *Euplotidium* Noland, 1937 and called the organism *Euplotidium agitatum* Noland, 1937 because of its erratic movements. Ito (1958) also described a cylindrical *Euplotes*-like organism, but in this species there was one left caudal cirrus and more frontoventral and transverse cirri than in *E. agitatum*, this he called *Euplotidium itoi* Ito, 1958. A further species with different numbers of frontoventral and transverse cirri, *Euplotidium arenarium* Magagnini & Nobili, 1964, was later described and Borror (1972) transferred *Euplotes psammophilus* Vacelet, 1961 to the genus. More recently Hartwig (1980) added another species to the genus.

Diagnosis of *Euplotidium*

Small to large (65–200 μm long) marine hypotrichs. Outline shape slightly elongated oval. Rounded in cross-section, never dorsoventrally flattened. The peristome is a wide funnel-shape with a prominent AZM that borders both the anterior semi-circular body edge and the left margin of the peristome. There are 7–12 frontoventral, 5–6 transverse and, when present, a reduced number (1–2) of caudal cirri.

Key to the species of *Euplotidium*

1	With less than 10 frontoventral cirri	2
	With 10 or more frontoventral cirri	4
2	With 9 frontoventral cirri but without caudal cirri	***E. agitatum***
	With 7 frontoventral and 1 or 2 caudal cirri	3
3	With 1 caudal cirrus, macronucleus in many parts	***E. helgae***
	With 2 caudal cirri, macronucleus elongate	***E. psammophilus***
4	With 10 frontoventral and more than 1 caudal cirri	***E. arenarium***
	With 12 frontoventrals and 1 caudal cirrus	***E. itoi***

Species descriptions

Euplotidium agitatum Noland, 1937

Description (Fig. 40). This, the type species, is 65–95 μm long and its cylindrical body shape is most apparent when viewed from the anterior. There is a funnel-shaped peristome which is lined around its anterior rim and left side by a prominent AZM. There are approximately 40 membranelles on the anterior part and about the same number in the

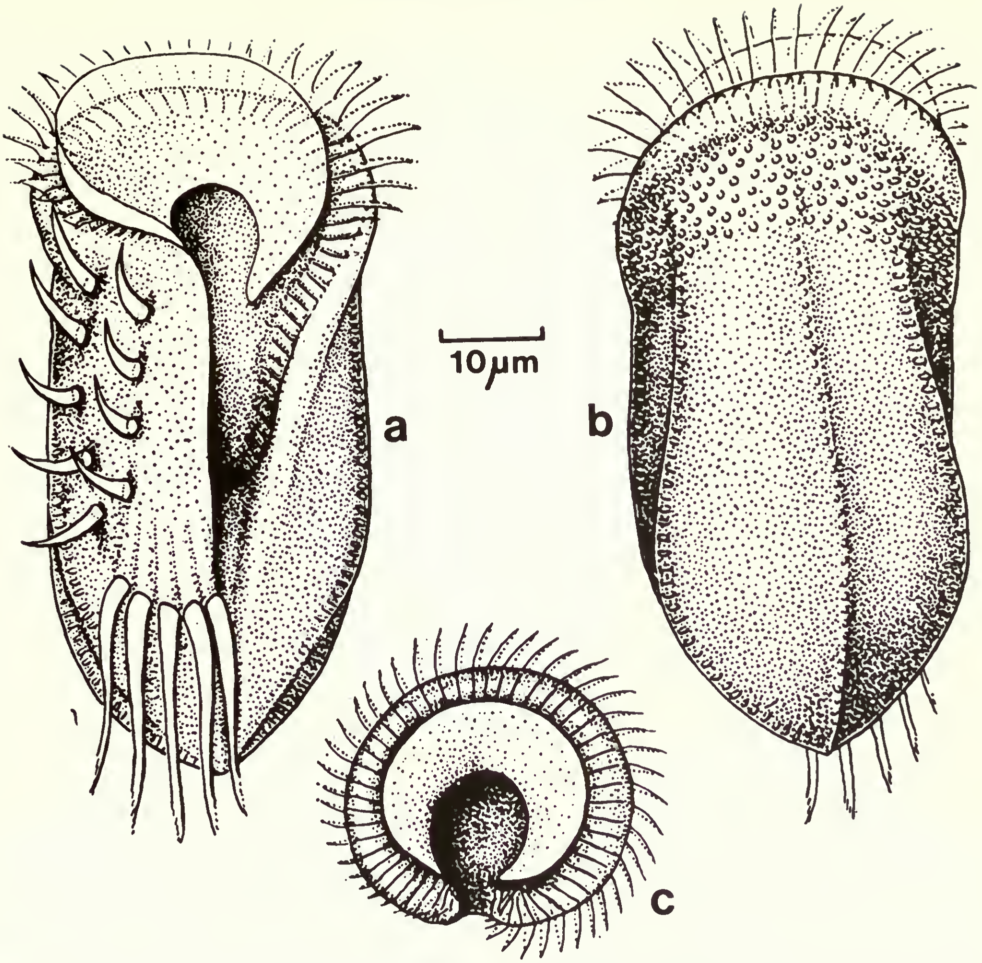

Fig. 40 *Euplotidium agitatum*, after Noland, 1937: (a) ventral surface; (b) dorsal surface; (c) view from anterior showing cylindrical body.

ventral part of the AZM. There are 9 frontoventral cirri, aligned in 2 rows, near the right body edge and 5 conspicuous transverse cirri but caudal cirri are not present.

Note. Originally isolated from water squeezed from sponges in the Gulf of Mexico.

Euplotidium itoi Ito, 1958

Description (Fig. 41). This is a medium sized (89–95 μm long), cylindrical hypotrich with a slightly flattened ventral surface. The AZM borders the anterior and left edges of the peristome forming a sigmoid shape. Nine of the 12 frontoventral cirri are in 2 oblique rows situated near the anterior right of the peristome while the other 3 are scattered along the right body edge. There are 6 large transverse cirri and a single small left caudal cirrus. The macronucleus is in 2 ribbon-like parts with 4 micronuclei.

Notes. The position of the reorganisation band in Ito's (1958) diagram indicates that it could have been at some stage of division. Originally found in seaweed in the Inland Sea of Japan.

Euplotidium arenarium Magagnini & Nobili, 1964

Description (Fig. 42). This is a medium sized (71–120 μm long) oval species with a wide

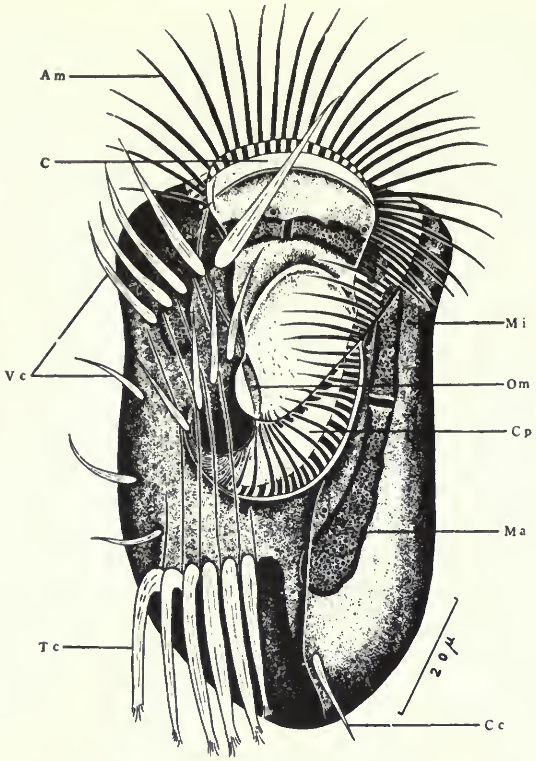

Fig. 41 *Euplotidium itoi*, after Ito, 1958.

triangular peristome. The AZM consists of about 75 membranelles and it extends around the anterior semi-circular rim of the peristome down to the left side. There are 10 frontoventrals, 5 transversals and a single left caudal cirrus. The transverse cirri are not conspicuous as in the other species of the genus and could be overlooked. The macronucleus is moniliform, in 5–10 pieces, and is curved towards the right. The silver-line system consists of 2 marginal kineties confluent posteriorly and there are dorsal and ventral mesh-like argyromes.

NOTE. Originally isolated from sand in the Gulf of Naples.

Euplotidium psammophilus (Vacelet, 1961) Borror, 1972

Euplotes psammophilus Vacelet, 1961

DESCRIPTION (Fig. 43). This is a large (125 μm long) species in which the wide peristome extends about two-thirds down the length of the body. There are 7 frontoventral cirri arranged in 2 groups on the right of the peristome. Three are closely packed together at the anterior and 4 are in a row behind them. The 5 transverse cirri are long and there are 2 caudal cirri. Vacelet (1961) also described the presence of a row of short cilia along the posterior right body edge. The elongated curved macronucleus is rod-like with an adjacent micronucleus.

NOTES. This was originally described as a species of *Euplotes*; Borror (1972) transferred it to *Euplotidium* on account of the shape of the body and peristome and because of the reduced number of caudal cirri.

Euplotidium helgae Hartwig, 1980

DESCRIPTION (Fig. 44). This is the largest (up to 200 μm long) of the species. The peristome

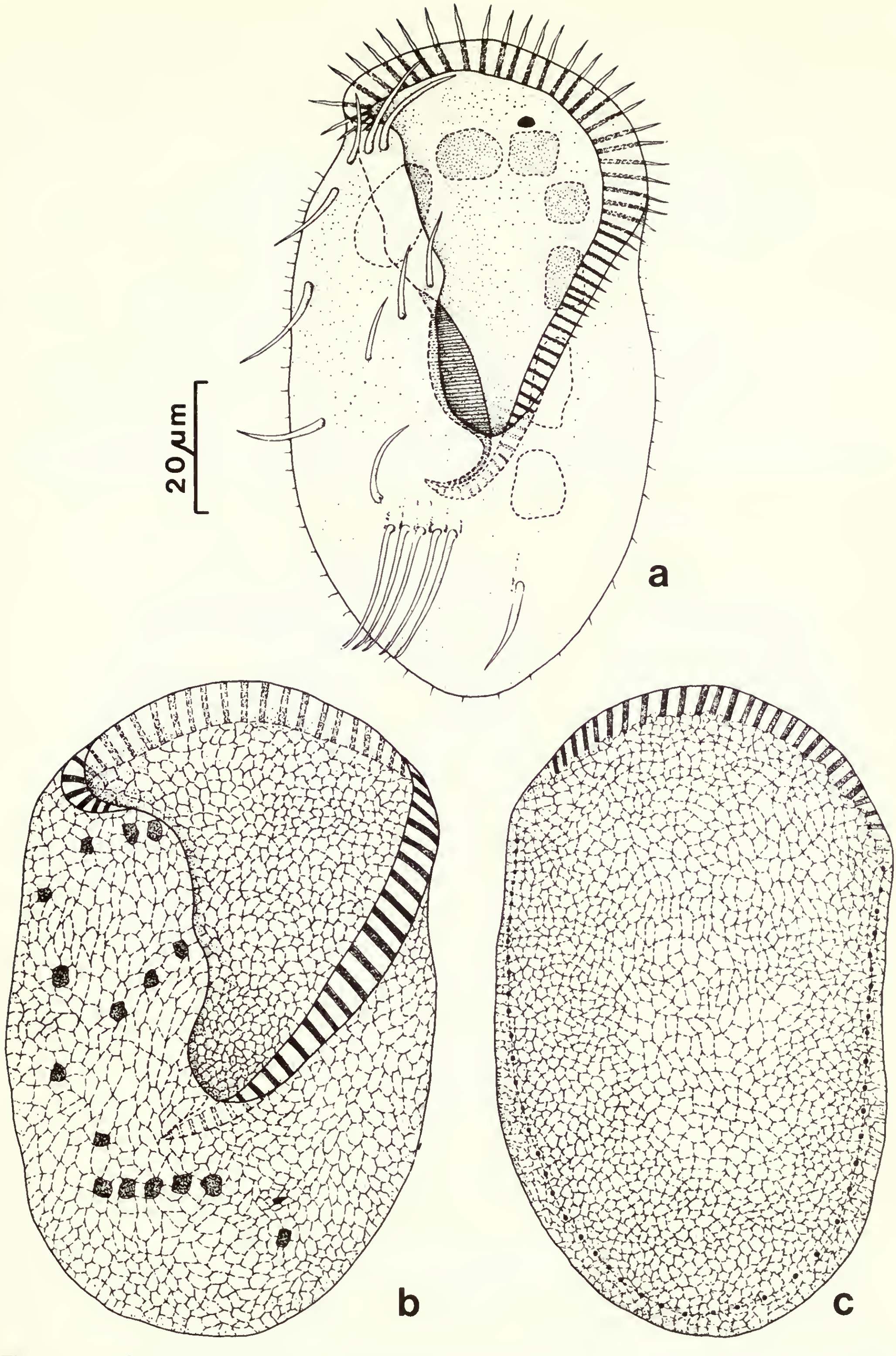

Fig. 42 *Euplotidium arenarium*, after Magagnini & Nobili, 1964; (a) ventral surface of living cell; (b, c) ventral and dorsal surfaces of silver-impregnated specimens; (d) stages in nuclear reorganisation.

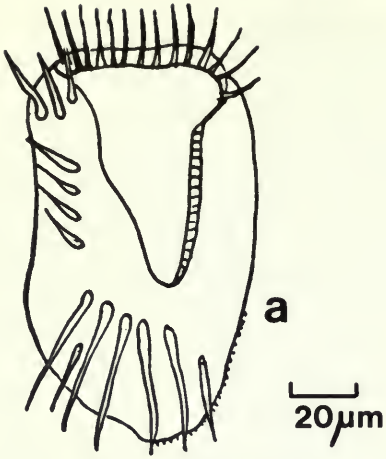

Fig. 43 *Euplotidium psammophilus*, after Vacelet, 1961 (called *Euplotes psammophilus*): (a) ventral surface; (b) nuclear apparatus.

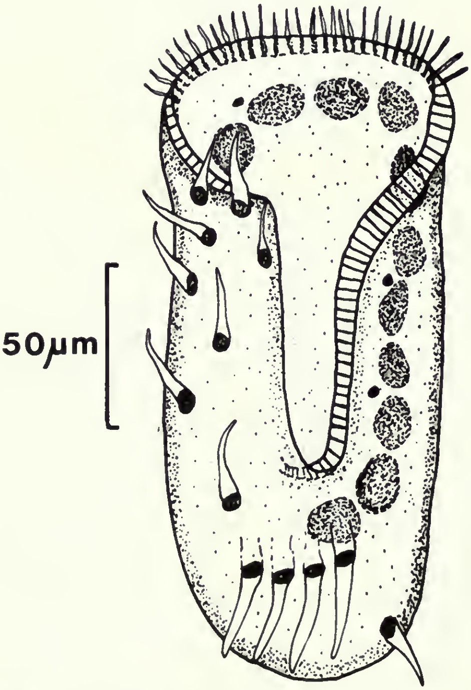

Fig. 44 *Euplotidium helgae*, after Hartwig, 1980.

extends about two-thirds down the body length. The original author (Hartwig, 1980) was not too sure about the cirral pattern and the interpretation used here is based on the assumption that there are 5 transverse and 7 frontoventral cirri rather than 4 transverse and 8 frontoventral cirri. There is a single caudal cirrus on the left and the frontoventrals are arranged in a single group on the right of the peristome. The macronucleus consists of 11 oval parts arranged in the shape of the letter C. There are several micronuclei.

NOTE. Originally found in sand in Bermuda.

Genus ***PARAEUPLOTES*** Wichterman, 1942

Introduction

Wichterman (1942) described a hypotrichous ciliate which he found in abundance on the coral *Eunicea crassa* in the Tortugas. The species resembled *Euplotes* in that it had a well developed AZM and a C-shaped macronucleus, but its rather peculiar ciliature bore no resemblance to that of *Euplotes*. He called the genus *Paraeuplotes* Wichterman, 1942 and placed it in a new family, the Paraeuplotidae Wichterman, 1942. Here, following Borror (1972) and Corliss (1977) the genus is provisionally included in the Euplotidae.

Diagnosis of *Paraeuplotes*

Discoid marine hypotrich with a well-developed AZM which originates on the dorsal surface and curves down three-quarters of the body length on the ventral surface. Undulating membrane absent. There are no marginal cirri but there is a small group of short caudal cirri. There is an extensive arc of transverse cirri parallel with the right body edge. Anteriorly, there is an arc of cilia parallel with the apical body edge and an isolated pair of cirri in the midventral position. The macronucleus is C-shaped. Contains numerous zooxanthellae.

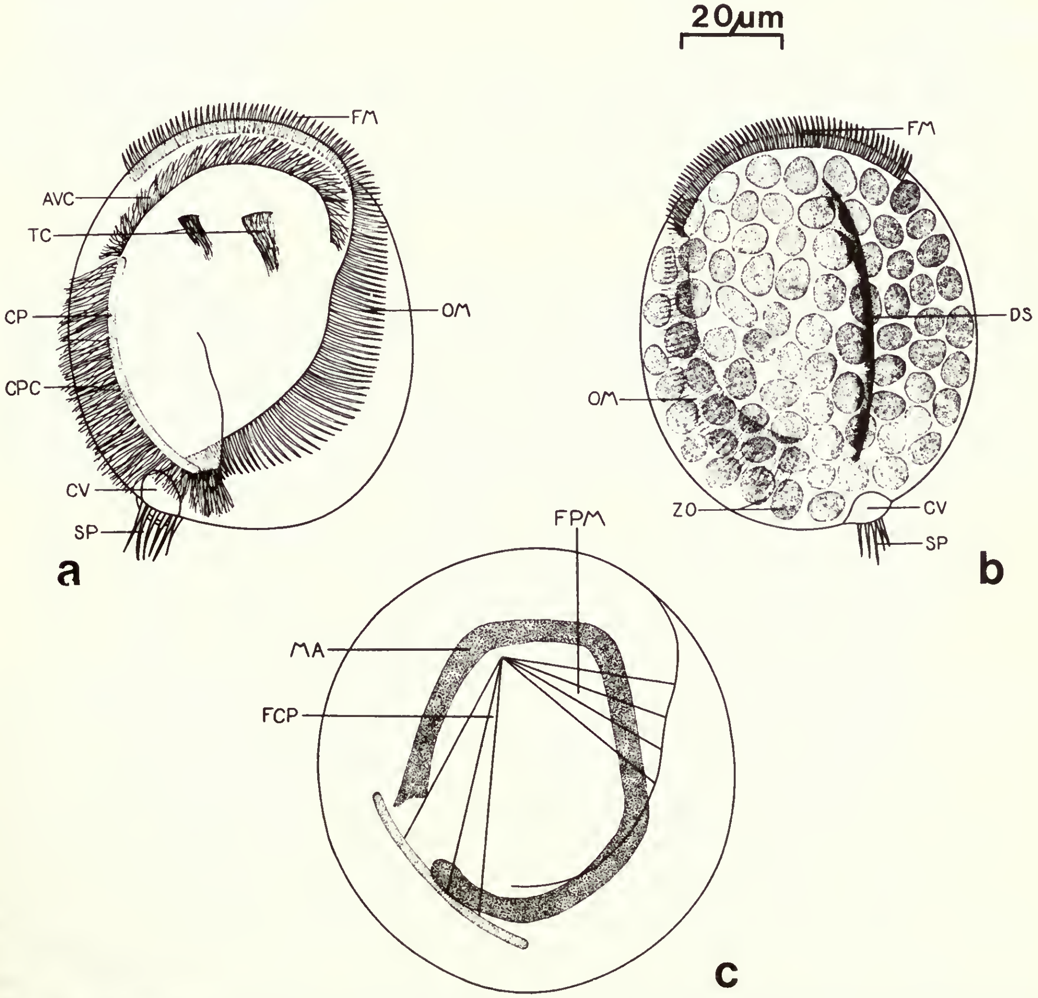

Fig. 45 *Paraeuplotes tortugensis*, after Wichterman, 1942: (a) ventral surface; (b) dorsal surface; (c) nucleus.

Species description

Paraeuplotes tortugensis Wichterman, 1942

Description (Fig. 45). Small to medium discoid species measuring on average 80 µm in diameter. The well-developed AZM forms a collar-like structure on the anterior dorsal surface which extends ventrally down about three-quarters of the body length. There is no undulating membrane present. Anteriorly there is an arc of cilia parallel with the body edge and a pair of isolated cirri lying in a midventral position. There is an extensive arc of transverse cirri parallel with the right body edge and a group of 5–6 short caudal cirri slightly to the right of the posterior body pole. The macronucleus is C-shaped. The cell is packed with numerous yellow-brown zooxanthellae.

Note. Originally isolated from the coral *Eunice crassa* in the Tortugas.

Genus ***SWEDMARKIA*** Dragesco, 1954

Introduction

Dragesco (1954, 1960, 1965) studied and described this genus over a period of several years. He (Dragesco, 1960, 1965) likened the genus to *Euplotidium* and *Gastrocirrhus* and considered it to be a possible evolutionary link between the Holostichidae Fauré-Fremiet, 1961 and the Euplotidae. Both Fauré-Fremiet (1961) and Corliss (1977) placed *Swedmarkia* in the family Gastrocirrhidae but it is here provisionally included in the Euplotidae.

Diagnosis of *Swedmarkia*

Medium sized (100–110 µm long) marine hypotrichs with conspicuous AZM arranged around a wide triangular peristome. There are two particularly long membranelles at the left of the apex of the peristome. A wide undulating membrane lies on the right of the peristome. There are many (54–58) cirri present with the following distribution. Numerous frontoventrals include a row along the right peristome edge, an apical group and an irregular midventral row. There are 5 large transverse and rows of right and left marginal cirri that are confluent posteriorly. The macronucleus is divided into numerous (about 100) portions and there are 5–9 micronuclei.

Species description

Swedmarkia arenicola Dragesco, 1954

Description (Fig. 46). This is a medium sized (100–110 µm long) marine hypotrich, similar in shape to *Euplotes*. The body is oval to triangular in shape and there is a large triangular peristome which extends down three-quarters of the body length where it occupies about half of the ventral surface. The AZM consists of 54–68 membranelles of which two, at the extreme left apex of the peristome, are particularly long. There is a wide undulating membrane on the right peristome border. The total of 54–58 cirri are arranged as follows, a row of frontoventral (peristomial) cirri is spaced evenly along the right peristomial edge. A group of 6 frontoventral cirri are situated around the extreme apex of the cell and there is an irregular row of 5 frontoventrals lying in the midventral position. Additionally, a short row of left marginal cirri is present with an irregularly spaced row of right marginals, of which the anterior half arise from the dorsal surface. The marginals are continuous along the posterior border. The macronucleus is divided into numerous (about 100) spherical pieces and there are 5–9 micronuclei. The three dorsal kineties bearing double cilia are illustrated in Fig. 46b.

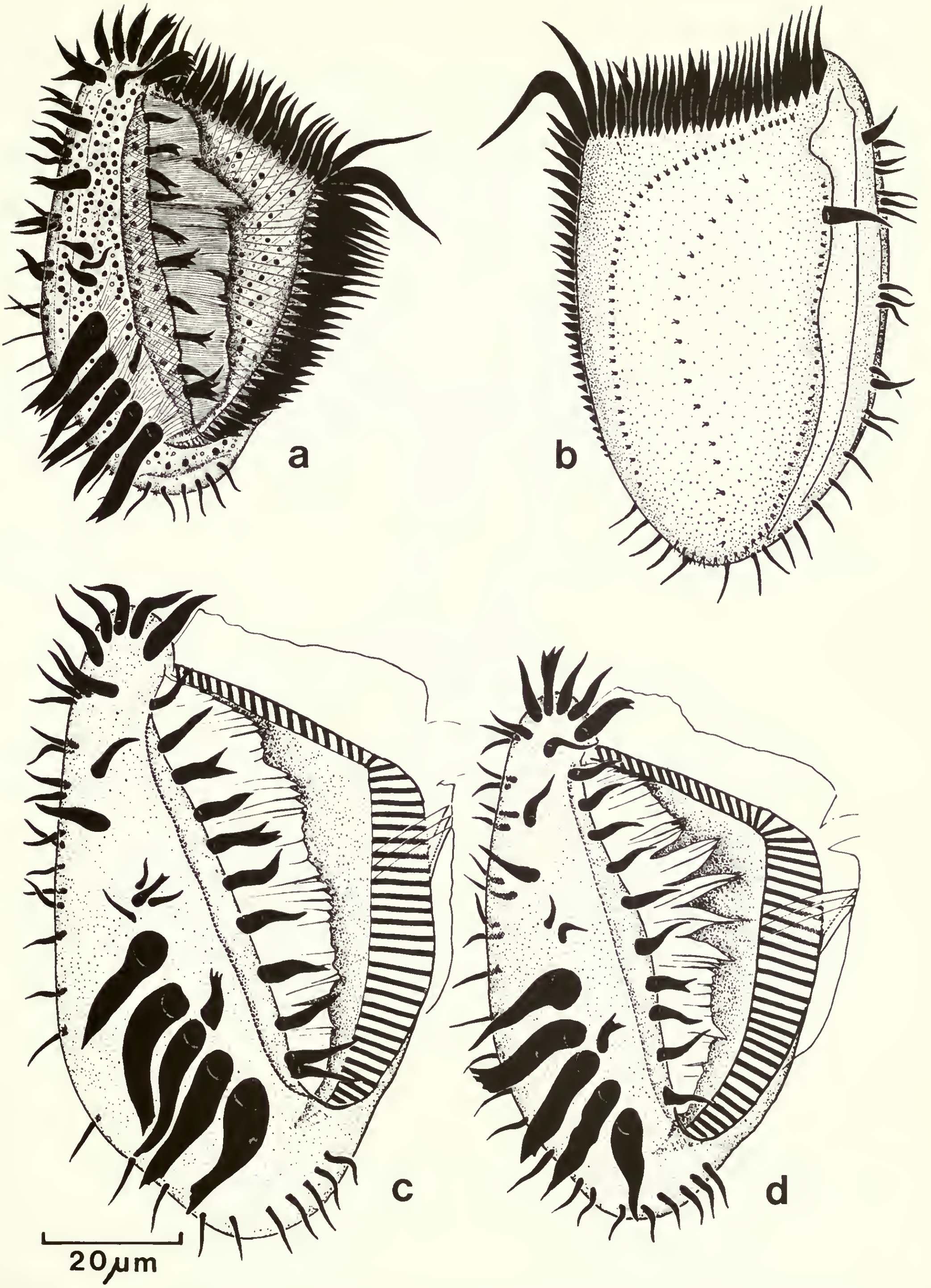

Fig. 46 *Swedmarkia arenicola*, after Dragesco, 1965: (a) ventral surface; (b) dorsal surface; (c, d) ventral surface showing variations in form, number and arrangement of certain cirri.

Genus *GRUBERELLA* (Gruber, 1884) Corliss, 1960

Stylocoma Gruber, 1884

Introduction

Gruber (1884) described the marine hypotrich *Stylocoma oviformis* Gruber, 1884 which Kahl (1932) redescribed and placed in the family Euplotidae. Soon after, another species, *Stylocoma adriatica* Kiesselbach, 1936, which lacked transverse cirri, was described. Corliss (1960) pointed out that the generic name was preoccupied by *Stylocoma* Lioy, 1864 a dipteran insect, and proposed that it should be replaced by *Gruberella* Corliss, 1960. Borror (1972) considered the genus to be of questionable status but Corliss (1977) included it as an *incertae sedis* in the Sporadotrichina. Here, the genus is provisionally included in the Euplotidae on account of its funnel-like peristome, which is reminiscent of *Gastrocirrhus*, and the arrangement of cirri which, although reduced, are more like those in the Euplotidae than in any other family of hypotrichs.

Diagnosis of *Gruberella*

Ovoid, marine hypotrichs, rounded in cross-section. There is a centrally placed funnel-shaped peristome bordered by a conspicuous AZM anteriorly and down the left side. Cirri reduced. Caudal cirri present, transverse cirri may or may not be present. Frontoventral and marginal cirri absent. Macronucleus in two parts.

Key to the species of *Gruberella*

1	With 6 caudal and 7 transverse cirri	***G. oviformis***
	With 6 caudal but without transverse cirri	***G. adriatica***

Species descriptions

Gruberella oviformis (Gruber, 1884) Corliss, 1960

Stylocoma oviformis Gruber, 1884

Description (Fig. 47). Ovoid marine hypotrich with wide, centrally placed, funnel-shaped peristome which has a slightly raised edge forming an anterior collar-like region. The

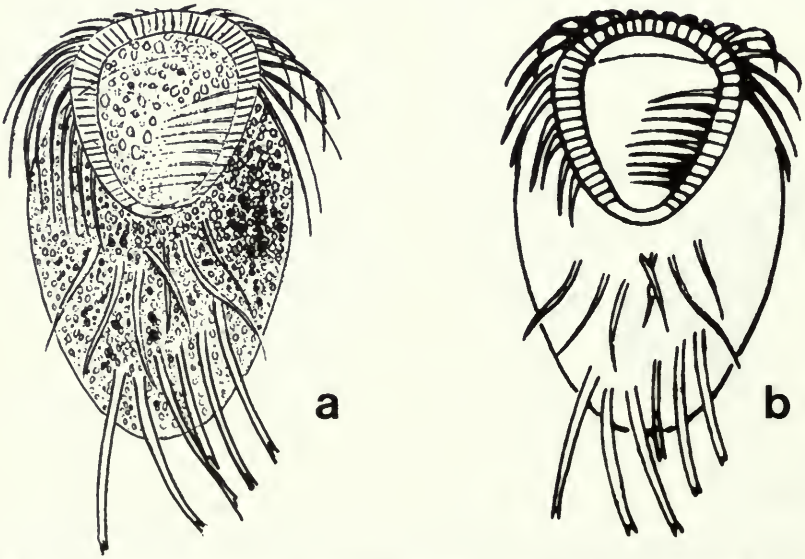

Fig. 47 *Gruberella oviformis*: (a) after Gruber, 1884; (b) after Kisselbach, 1936.

prominent AZM consisting of many large membranelles originates on the ventral surface on the right of the peristome and continues around the apex down the left side. There are only 2 groups of cirri, 7 transverse and 6 long caudal cirri. No frontoventral or marginal cirri are present. Shape of macronucleus unrecorded.

Gruberella adriatica (Kisselbach, 1936) Corliss, 1960

Stylocoma adriatica Kiesselbach, 1936

Description (Fig. 48). Medium sized (80 μm long) triangular shaped marine hypotrich with funnel-shaped, centrally positioned peristome. Prominent AZM borders the anterior and left peristomial edges. Cirri reduced to a single group of 6 long caudals. There are no transverse, frontoventral or marginal cirri present. Macronucleus divided into 2 ovoid pieces with a micronucleus between the pair.

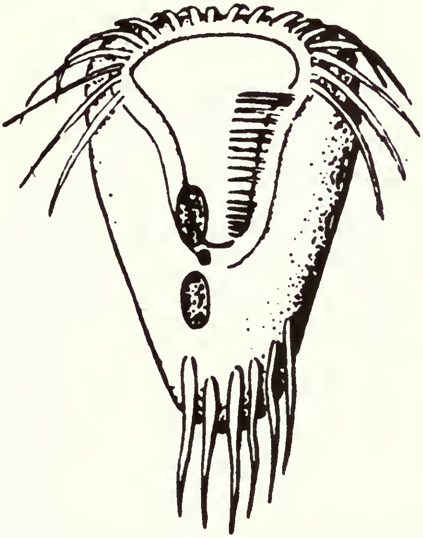

Fig. 48 *Gruberella adriatica*, after Kisselbach, 1936.

Genus *CYATHAROIDES* Tuffrau, 1975

Introduction

Tuffrau (1975) described a species from Antarctica which closely resembled *Euplotes* in certain respects but not in others. It is characterised by the presence of a row of 12 large right marginal cirri in addition to the usual frontoventral and transverse cirri. Furthermore, there is an extensive paroral membrane composed of a single kinety of long cilia which is unlike the undulating membrane of *Euplotes* and there is also endoral ciliature which is not found in *Euplotes*.

Diagnosis of *Cyatharoides*

Irregularly oval marine hypotrich with a very large peristomial funnel occupying much of the ventral surface onto which it opens. The peristome is surrounded by a collar-like swelling of the anterior left body edge, with a characteristic ‘niche’ or invagination of the right anterior peristome region. The AZM is composed of many membranelles lining the left peristomial border. On the right, at the bottom of the peristomial funnel there is a paroral membrane composed of a single kinety of long cilia and an arc of endoral cilia. There are 10 frontoventral, 5 transverse and a row of 12 right marginal cirri along the right body edge. Dorsally there are 12–26 kineties of cilia and the macronucleus is C-shaped.

Species description

Cyatharoides balechi Tuffrau, 1975

DESCRIPTION (Fig. 49). Irregularly oval, large (140–200 µm long) marine, planktonic hypotrich with a very large peristomial funnel opening over much of the ventral cell surface. Anteriorly the peristome is surrounded by a collar-like swollen ridge of the anterior left body edge, with a characteristic invagination of the peristome on the right anterior edge. The AZM is prominent and composed of many large membranelles. There are paroral and endoral membranes on the posterior right peristomial edge. With 10 frontoventral, 5 transverse and 12 right marginal cirri. Dorsal surface with 12–26 kineties of many cilia. Macronucleus large, open C-shaped.

NOTE. Originally isolated from plankton sample taken from Antarctic Ocean near base of Argentina by Prof. Balech.

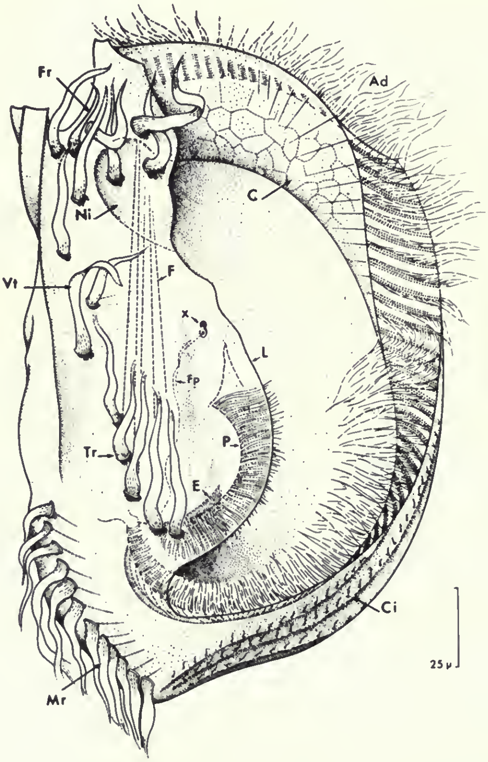

Fig. 49 *Cyatharoides balechi*, ventral surface, after Tuffrau, 1975.

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C. G. Ogden & R. H. Hedley

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Peter Humphry Greenwood

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Synopsis

The *Ophthalmotilapia* assemblage of cichlid fishes from Lake Tanganyika, first defined by Liem (1981), originally comprised the genera *Asprotilapia*, *Ectodus*, *Lestradea*, *Cunningtonia* and *Ophthalmotilapia* (with which was synonymized *Ophthalmochromis*). The characters on which the assemblage was based are reviewed and revised in the light of information derived from large-scale outgroup comparisons.

As a result of this review, five additional genera can be included in the assemblage (viz. *Aulonocranus*, *Grammatotria*, *Callochromis*, *Xenotilapia* and *Cyathopharynx* (with which *Cardiopharynx* is synonymized). Two lineages within the *Ophthalmotilapia* assemblage are defined.

Previous schemes of supposed relationships for these taxa are discussed, as is the problem of identifying the sister-group for the assemblage. No sister-group can be identified amongst the endemic taxa of Lake Tanganyika, but the possibility of an endemic taxon from Lake Malawi being the sister-group is explored.

Problems arising from possible homoplasy and thus the misidentification of sister-groups are illustrated by examples involving cichlid species from Lakes Tanganyika and Malawi, and from these lakes and Lake Fwa (Zaire drainage basin).

Introduction

During the last thirty years there has been a marked increase in our knowledge of taxonomic and ecological diversity amongst African cichlid fishes. Unfortunately there has been less progress made in our understanding of phyletic relationships between the various elements of those faunas, or even amongst members of the so-called species flocks of the major African lakes (see Greenwood, 1980).

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Two recent papers are welcome and important contributions to the field of phyletic studies since both are concerned with interrelationships in a single species flock, that of Lake Tanganyika (Liem & Stewart, 1976; Liem, 1981).

Liem's (1981) paper is directed at establishing the monophyletic origin of five endemic genera from that lake, viz. *Asprotilapia, Ectodus, Lestradea, Cunningtonia* and *Ophthalmotilapia.* Although Liem was able to argue a case for recognizing the monophyly of these taxa (the *Ophthalmotilapia* assemblage), and the intragroup relationships of its constituent genera, he was unable to recognize a sister-group for the whole assemblage. He did, however, suggest that among the endemic Tanganyika genera, *Aulonocranus, Xenotilapia, Callochromis* and *Cardiopharynx* share some of the derived features characterizing the *Ophthalmotilapia* assemblage (Liem, 1981 : 206; 208).

My interest in these species, and the *Ophthalmotilapia* lineage, stems from my current research into the levels of relationship existing between the endemic cichlid genera of Lakes Victoria, Malawi and Tanganyika (Greenwood, 1979; 1980). Using information acquired in this search, it seemed that Liem's concept of the *Ophthalmotilapia* assemblage could be extended to include several other Tanganyika taxa, including those suspected of such relationship by Liem. It was also apparent that the group characters for the assemblage should be reviewed in the light of more extensive outgroup comparisons than were employed originally.

Finally, my interest was aroused by what seemed to be the unusually clear light that some members of the *Ophthalmotilapia* assemblage could throw on the longstanding and often intractable problem of homoplasy and its effects on hypotheses of relationship amongst African cichlid fishes.

Like Liem, I have been unable to identify a sister-group for the *Ophthalmotilapia* assemblage from amongst the Tanganyika cichlids. A very tentative suggestion can be made, however, for a possible sister-group relationship between the assemblage and certain members of the Lake Malawi flock.

Material examined

Dissections were made of the dorsal gill-arch musculature in one, or usually 2, specimens of each genus now included in the *Ophthalmotilapia* assemblage (see p. 278). The specimen of *Asprotilapia leptura* (BMNH 1906.9.6 : 157) was that used by Liem (1981) but the jaw muscles of the left side were freshly dissected.

The nature of the gut and its coiling pattern were checked in several specimens of each *Ophthalmotilapia* assemblage species (except *Asprotilapia leptura* where only the type and the specimen noted above could be used).

Jaw and dorsal gill-arch muscles were dissected in unregistered specimens of *Astatotilapia elegans* and in *A. burtoni.*

All available dry skeletal material in the BM(NH) collections was examined, in particular that prepared for the revisions of the Lake Victoria, Edward-George, Kivu, and Turkana haplochromine species (see Greenwood, 1980). Additional material, prepared for this paper, and alizarin transparencies not previously listed, are given below. The taxa are first grouped geographically, and then alphabetically, within the categories: Dry skeleton (DS) and Alizarin transparency (AT).

Lake Tanganyika

DS:

Asprotilapia leptura	671
Aulonocranus dewindti	1960.9.30 : 4629–641
Callochromis macrops	1906.9.8 : 178
Cardiopharynx schoutedeni	1950.4.1. : 1854–81; 1960.9.30 : 1647–56
Cyathopharynx furcifer	1900.9.8 : 251; 148; 1950.4.1 : 1714–47

Cunningtonia longiventralis	1950.4.1 : 1265–1281
Ectodus descampsi	1906.9.8 : 194; 1950.4.1 : 3066–67
Eretmodus cyanostictus	1950.4.1 : 5171–82; 693
Grammatotria lemairei	1950.4.1 : 3758–3785
Lestradea perspicax stappersi	1960.9.30 : 1553–1557
Limnochromis auritus	1906.9.6 : 71
Limnochromis leptosoma	1906.9.6 : 83
Lobochilotes labiatus	1950.4.1 : 554–566; 567–579; 590–606
Neotilapia tanganicae	1900.12.13 : 35
Ophthalmotilapia boops	1960.9.30 : 1720–1724
Ophthalmotilapia ventralis	1906.9.8 : 144
Perissodus microlepis	Uncatalogued
Perissodus paradoxus	1906.9.8. : 267
Petrochromis famula	1950.4.1 : 7642–52
Petrochromis fasciolatus	1960.9.30 : 1368–71; 1372–75
Petrochromis polyodon	1898.9.9 : 66; 1950.4.1 : 7608–611; uncatalogued
Simochromis babaulti	Uncatalogued
Simochromis curvifrons	1955.4.12 : 47–66; uncatalogued
Simochromis dardennei	1906.9.8 : 244; uncatalogued (4 specimens)
Simochromis diagramma	1906.9.8 : 217; uncatalogued
Simochromis loocki	1950.4.1 : 7674–7701; 7702–7728
Trematocara marginatum	1960.9.30 : 4835–4850
Trematocara unimaculatum	1906.9.6 : 119
Tropheus moorei	1950.4.1 : 907–67; uncatalogued
Xenotilapia boulengeri	1961.11.22 : 290–293

AT:

Astatotilapia burtoni	1960.9.30 : 2415–33
Aulonocranus dewindti	1950.4.1 : 4695–775; 4642–656
Callochromis macrops macrops	1960.9.20 : 2821–2823
Callochromis macrops melanostigma	1960.9.30 : 2845–2859
Cardiopharynx schoutedeni	1960.9.30 : 1574–1615
Ctenochromis horei	1960.9.30 : 2526–28
Cunningtonia longiventralis	1960.9.30 : 1896–1907
Cyathopharynx furcifer	1960.9.30 : 1792–1802
Ectodus descampsi	1961.11.22 : 113–119
Eretmodus cyanostictus	1950.4.1 : 5171–5182
Grammatotria lemairei	1960.9.30 : 3317–30; 3276–79; 3208–21
Hemibates stenosoma	1961.11.22 : 976–989
Lamprologus brevis	1960.9.30 : 7181–7225
Lamprologus cunningtoni	1950.4.1 : 6701–6707
Lamprologus elongatus	1960.9.30 : 6851–6860
Lamprologus fasciatus	1950.4.1 : 7075
Lamprologus tetracanthus	1960.9.30 : 7309–7336
Lamprologus werneri	1976.5.21 : 46–65
Lestradea perspicax	1960.9.30 : 1468–84
Limnochromis abeelei	1961.11.22 : 56–58
Limnochromis auritus	1960.9.30 : 1981–85
Limnochromis dhanisi	1960.9.30 : 2001–04
Limnochromis otostigma	1960.9.30 : 1989–97
Limnochromis pfefferi	1960.9.30 : 1923–26
Limnochromis permaxillaris	1961.11.22 : 41–46
Ophthalmotilapia boops	1960.9.30 : 1716–18; 1720–24
Ophthalmotilapia ventralis	1960.9.30 : 1689–94
Perissodus hecqui	1960.9.30 : 6364–69
Perissodus microlepis	1960.9.30 : 6386–91
Perissodus paradoxus	1960.9.30 : 6468–6482
Petrochromis fasciolatus	1960.9.30 : 1392–93; 1394–96; 1390
Petrochromis polyodon	1960.9.30 : 1359–63

Simochromis curvifrons	1961.11.22 : 2–8
Simochromis dardennei	1960.9.30 : 1061
Simochromis diagramma	1960.9.30 : 1170–1174; 1188–91
Simochromis loocki	1950.4.1 : 7702–28
Telmatochromis temporalis	1960.9.30 : 6531–6538
Trematocara caparti	1961.11.22 : 703–721
Trematocara kufferathi	1961.11.22 : 883–910
Trematocara marginatum	1960.9.30 : 4881–90
Trematocara nigrifrons	1961.11.22 : 693–703; 1960.9.30 : 4990–5019
Trematocara stigmaticum	1960.9.30 : 5143–171
Trematocara unimaculatum	1961.11.22 : 519–528
Tropheus moorei	1961.11.22 : 13
Xenotilapia boulengeri	1961.11.22 : 225
Xenotilapia melanogenys	1950.4.1 : 4035–40; 1960.9.30 : 3449–455
Xenotilapia ochrogenys	1960.9.30 : 3820–855
Xenotilapia sima	1961.11.22 : 208–211
Xenotilapia tenuidentata	1960.9.30 : 7998–8014

Lake Malawi

DS:

Astatotilapia calliptera	1893.11.15 : 4
Aulonocara nyassae	1935.6.14 : 2259–63; 681.5A
Aulonocara rostrata	681.5A
Chilotilapia rhoadesii	681.2; 1935.6.14 : 2103–211
Corematodus shiranus	681.4A
Corematodus taeniatus	681.4B; 681.4C
Cyathochromis obliquidens	1935.6.14 : 282–295; 681.12A : 681.12B
Cynotilapia afra	1893.1.17 : 8 (syntype)
Docimodus johnstoni	681.3
Genyochromis mento	1965.10.26 : 24–29
Gephyrochromis lawsi	1965.11.2 : 14–22 (paratypes)
'Haplochromis' ahli	1935.6.14 : 1469–71
'Haplochromis' annectens	1935.6.14 : 847–52
'Haplochromis' argyrosoma	1935.6.14 : 1657–61
'Haplochromis' atritaeniatus	1935.6.14 : 1426–9
'Haplochromis' auromarginatus	1935.6.14 : 1476–78
'Haplochromis' breviceps	1935.6.14 : 870–72
'Haplochromis' caeruleus	1935.6.14 : 1267–69
'Haplochromis' chrysonotus	1935.6.14 : 1823–32
'Haplochromis' dimidiatus	1935.6.14 : 1154–71
'Haplochromis' ericotaenia	1935.6.14 : 2405–2411
'Haplochromis' euchilus	1972.9.13 : 70
'Haplochromis' eucinostomus	1962.10.18 : 1–10
'Haplochromis' fuscotaeniatus	1935.6.14 : 494–95
'Haplochromis' guentheri	1921.9.6 : 154–62
'Haplochromis' intermedius	1972.9.13 : 91–94
'Haplochromis' johnstoni	1935.6.14 : 523–32
'Haplochromis' kirkii	1935.6.14 : 953–62
'Haplochromis' kiwinge	1935.6.14 : 1031–40
'Haplochromis' labifer	1972.9.13 : 77–81
'Haplochromis' labridens	1935.6.14 : 991–1000; 1001–05
'Haplochromis' lateristriga	1935.6.14 : 1209–18
'Haplochromis' lepturus	1935.6.14 : 1340–56
'Haplochromis' longimanus	1972.12.20 : 35–78
'Haplochromis' macrostoma	1935.6.14 : 605–7
'Haplochromis' marginatus	1935.6.14 : 769–77
'Haplochromis' moorii	1935.6.14 : 1692–1700
'Haplochromis' nototaenia	1935.6.14 : 1378–84
'Haplochromis' ornatus	1972.12.18 : 31–33

'Haplochromis' orthognathus	1973.3.26 : 189; 1969.3.11 : 19
'Haplochromis' placodon	1935.6.14 : 1736–45
'Haplochromis' pleurotaenia	1935.6.14 : 911–16
'Haplochromis' polystigma	1935.6.14 : 433–37
'Haplochromis' quadrimaculatus	1935.6.14 : 1960–69
'Haplochromis' prostoma	1962.10.18 : 59–71; 1979.11.26 : 5–9
'Haplochromis' rhoadesii	681T
'Haplochromis' rostratus	1935.6.14 : 549–54
'Haplochromis' semipalatus	1956.6.12 : 9–10
'Haplochromis' spilonotus	1969.3.11 : 11–14
'Haplochromis' spilorhynchus	1935.6.14 : 1260–4
'Haplochromis' subocularis	1935.6.14 : 1180–89
'Haplochromis' tetrastigma	1935.6.14 : 1556–66; 1567–77
Hemitilapia oxyrhynchus	1906.9.7 : 39
Labeotropheus fuelleborni	1972.8.11 : 3–5; 681.11
Labidochromis vellicans	1965.10.26 : 14–21
Labidochromis zebroides	1981.1.9 : 102–106 (paratype)
Lethrinops auritus	1930.1.31 : 84–86
Lethrinops lethrinus	1930.1.31 : 150–4; 1906.9.7 : 35
Lethrinops longimanus	1969.3.11 : 20–23
Lethrinops parvidens	1935.6.14 : 2070–73
Lethrinops praeorbitalis	696J
Melanochromis melanopterus	1935.6.14 : 303 (syntype); 1971.9.13 : 32–36
Melanochromis vermivorous	1935.6.14 : 307–16 (syntype)
Petrotilapia tridentiger	1981.2.2 : 212–20; 681.9
Pseudotropheus fuscus	1965.10.25 : 131–41
Pseudotropheus livingstoni	1935.6.14 : 128–30
Pseudotropheus lucerna	1935.6.14 : 165–9 (syntype)
Pseudotropheus macrophthalmus	Uncatalogued
Pseudotropheus tropheops	1965.10.25 : 115–24; 681.8C
Pseudotropheus williamsi	1965.10.25 : 20–26; 681.8B
Pseudotropheus zebra	1935.6.14 : 135–40; 681.8A
Trematocranus microstoma	1935.6.14 : 2232–6

AT:

Astatotilapia calliptera	1966.7.26 : 17–42
Aulonocara nyassae	1935.6.14 : 2259–63
Lethrinops lethrinus	1930.1.31 : 109–118

Elsewhere

DS:

Astatotilapia bloyeti	1961.12.1 : 341–353
Astatotilapia nubila	1911.3.3 : 148
Chromidotilapia batesii	1912.6.29 : 4
Chromidotilapia kingsleyae	1912.4.1 : 526; 1908.5.30 : 186
Oreochromis niloticus	662D; Uncatalogued
Tilapia rendalli	1906.9.7 : 32
Tilapia zilli	1907.12.2 : 3767

AT:

Astatotilapia bloyeti	Uncatalogued
Astatotilapia macropsoides	Uncatalogued
Oreochromis niloticus	1907.12.2 : 3533–534

Radiographs used in this study were:

Lake Tanganyika

Asprotilapia leptura	1906.9.6 : 156–157 (FW 677)
Aulonocranus dewindti	1950.4.1 : 4843–93 (FW678)
Callochromis macrops macrops	1950.4.1 : 3258–312 (FW683)

Callochromis macrops melanostigma	1960.9.30 : 2882–96 (FW683)
Callochromis pleurospilus	1940.4.1 : 3458–662; 1920.5.25 : 152–53 (FW682)
Cardiopharynx schoutedeni	1960.9.30 : 1574–1615 (FW674)
Cunningtonia longiventralis	1950.4.1 : 1282–86 (FW676)
Cyathopharynx furcifer	1950.4.1 : 1605–37; 1906.9.8 : 249–251 (FW673)
Ectodus descampsi	1961.11.22 : 76–87 (FW677)
Grammatotria lemairei	1950.4.1 : 3703–3727 (FW684)
Lestradea perspicax	1950.4.1 : 1531–46 (FW676)
Ophthalmotilapia boops	1960.9.30 : 1720–24 (FW675)
Ophthalmotilapia ventralis	1950.4.1 : 1291–1465 (FW675)
Xenotilapia boulengeri	1961.11.22 : 290–93 (FW679)
Xenotilapia melanogenys	1960.9.30 : 3419–48 (FW681)
Xenotilapia ochrogenys	1950.4.1 : 4047–136 (FW679)
Xenotilapia ornatipinnis	1960.9.30 : 3685–728 (FW681)
Xenotilapia sima	1961.11.22 : 190–202 (FW680)
Lake Fwa	
Callopharynx microdon	MRAC 71300 (FW671)
Cyclopharynx fwae	MRAC 71301 (FW671)
Neopharynx schwetzi	MRAC 71290, 76201 (FW671); 71291–99 (FW672)

A review of group characters for the *Ophthalmotilapia* assemblage

As originally defined by Liem (1981), the *Ophthalmotilapia* assemblage[1] comprised the following genera: *Asprotilapia* Blgr (1901), *Ectodus* Blgr (1898), *Lestradea* Poll (1943), *Cunningtonia* Blgr (1906) and *Ophthalmotilapia* Pellegrin (1904). *Ophthalmochromis* Poll (1956) was shown by Liem (1981 : 210) to be a synonym of *Ophthalmotilapia,* a decision with which I fully agree.

Liem's concept of the *O*A, and his grounds for considering it a monophyletic group, were based on eight uniquely congruent apomorphic characters present in all the constituent taxa (Liem, 1981 : 207–208). With one possible exception, however, Liem believed that none of these characters is an autapomorphy for the group (Liem's character 2, the outline shape of the palatine bone, is the exception).

The apomorphic status of the eight group-characters was justified by Liem (1981 : 205) on the grounds of their being derived relative to the character state found in various generalized taxa (such as *Astatotilapia burtoni* and *A. elegans*) and in other taxa from Lake Tanganyika.

I have been able to extend Liem's outgroup comparisons to include the cichlid genera of Lakes Malawi, Victoria and Edward, taxa from various river systems and their associated small lakes, and additional genera from Lake Tanganyika itself. Wherever possible, several species of a genus were examined.

The review of the eight *O*A group-characters which follows takes this extra material into account. It should be noted, however, that the new members of the *O*A (see p. 262) are, for the purposes of the review, not treated as elements of the assemblage. Thus, unless otherwise indicated, all references to the *O*A in this section of the paper are to the assemblage as originally defined by Liem.

Since the sequence in which group apomorphies are treated here differs somewhat from that used by Liem (1981 : 207), the number he gave to a character is given, in square brackets, after the number used in this review. The same convention is followed throughout the paper.

(1) [1]. The entopterygoid is widely separated from the palatine (see Liem, 1981 : 205–206, 207; fig. 4; and Figs 1A–F below).

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[1] For the sake of brevity, Liem's shorthand term for the assemblage, the *O*A, will be used in this paper as well.

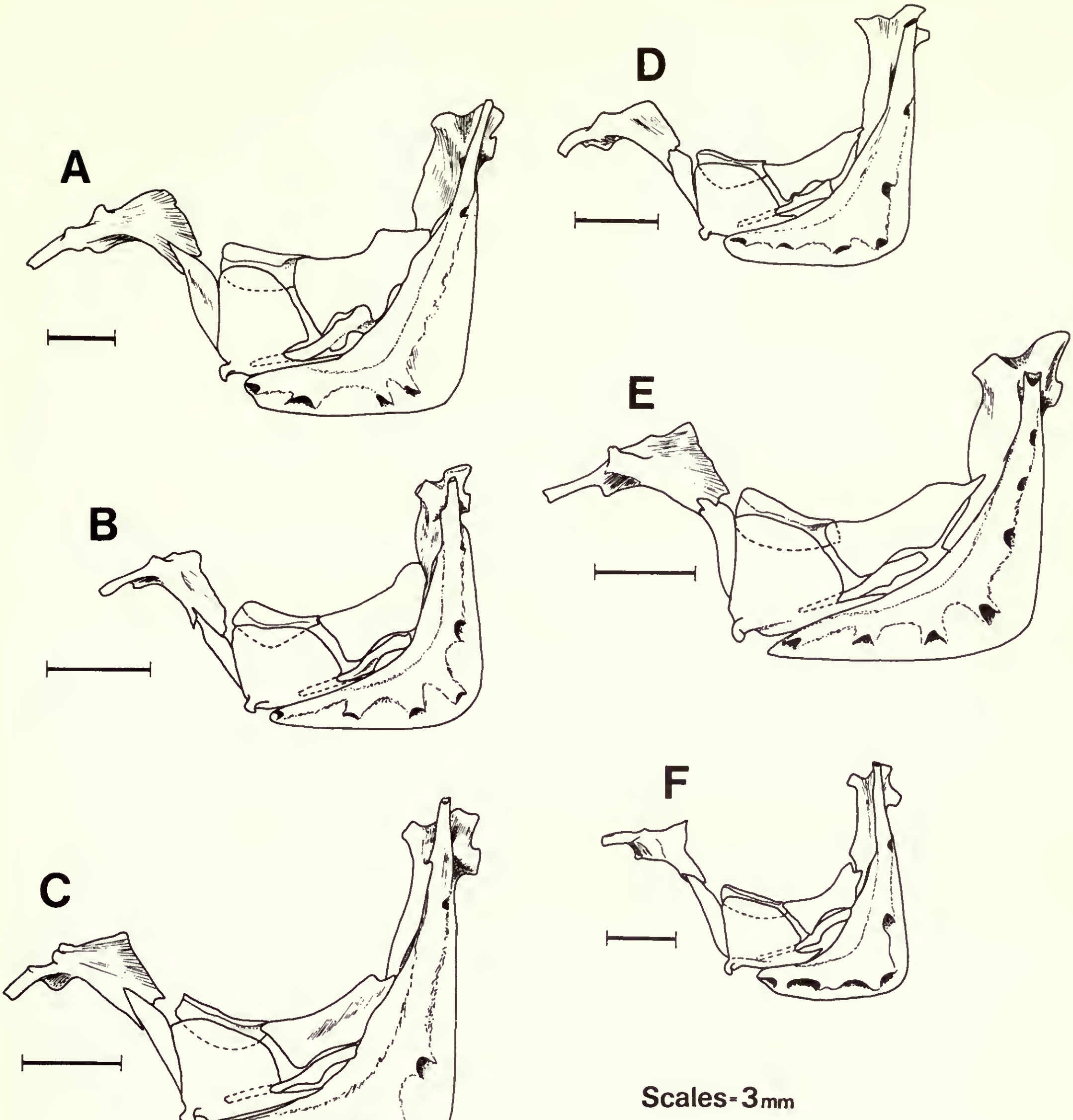

Fig. 1 Suspensoria (left) of: A, *Callochromis macrops melanostigma*; B, *Xenotilapia tenuidentata*; C, *Cyathopharynx furcifer*; D, *Cyathopharynx schoutedeni* (see p. 282); E. *Grammatotria lemairei*; F, *Aulonocranus dewindti.*

As far as I can determine, this character, except for its occurrence in the Malawian genus *Lethrinops* (and those species from Tanganyika which I propose to include in the *O*A) is unique to the *Ophthalmotilapia* assemblage.

The gap is created, in part, by a reduction in the depth of the entopterygoid, and in part by a reduction of its extension above the quadrate. As a result of these proportional and positional changes, the anterior entopterygoidal margin lies below the level of the palatine's posterior margin, and below the upper part of the ectopterygoid as well (with both of which bones it would otherwise articulate). The space between the three bones (that is, the 'gap') is actually filled by dense, translucent connective tissue.

It could be argued (and has been argued by Barel, *pers. comm.*) that the palatopterygoid gap is a correlate of the large and often ovoid eye characterizing all members of the *O*A. This is a complex problem to resolve since the influence of eye size and shape on cranial architecture is the result of several interacting factors, and there are few data available on the dynamics of syncranial ontogeny. In particular we have no information on the influence of ultimate eye size on the ontogeny of the whole suspensorium, of which the palatine and entopterygoid bones are but a part (see below p. 257).

Taking the maximum diameter of the eye (expressed as a proportion of head length) as a measure of eye size it is difficult to find a simple correlation between that ratio and the nature of the palatine-entopterygoid articulation. For example, in *Hemibates, Trematocara, Reganochromis*, certain '*Limnochromis*' species and in *Perissodus* (all from Lake Tanganyika) the eye is as large as that in members of the *O*A, and the eye in *Trematocara* is as markedly ovoid as it is in any member of the *O*A. Yet, in none of these species is there a palatopterygoid gap. (Recently, Poll (1981) has revised the genus *Limnochromis* which he now divides into four genera. Since several of the older references in the literature are just to the genus *Limnochromis*, I have adopted the convention of referring to the taxon as '*Limnochromis*', except when reference is made to species retained by Poll (1981) in that genus.)

Conversely, in many species of the Malawian genus *Lethrinops* (Fig. 15) there is a palatopterygoid gap (albeit a less extensive one than in some though not all *O*A species), but the eye is smaller than in members of the *O*A.

Since, amongst the taxa with enlarged eyes only the *O*A species have developed a palatopterygoid gap, the gap would seem to be a shared derived character for the assemblage.

That argument would hold even if future research shows the 'gap' to be one of several correlated features associated with the evolution of a large eye. The presence of a gap in *Lethrinops* (which does not have enlarged eyes), on the other hand, fails to support any argument suggesting that eye size and a palatopterygoid gap are necessarily correlated.

(2) [3]. The slender hyomandibula has a long symplectic process and no, or a very reduced, hyomandibular flange.

On the basis of extensive outgroup comparisons I cannot agree with Liem on the relative length of the symplectic process. In fact, most *O*A species have a process which is no longer than that in *Astatotilapia burtoni, A. elegans* (or in other *Astatotilapia* species), or that in other Tanganyika genera (Fig. 2). Unfortunately this character is difficult to quantify and is one affected by the level to which the anterior margin of the hyomandibular flange is produced ventrally. To this extent the apparent length of the process is an optical illusion. It is also affected by the stoutness of the flange which, in this region of the bone, is easily damaged; if partially broken its absence may add to the apparent length of the symplectic process.

As compared with the hyomandibular flange in many taxa (both within and outside Lake Tanganyika) that in all *O*A species is reduced. But, I would question that it is ever absent, even in those species with the greatest reduction in flange area.

A reduction in flange area comparable with that found in *O*A species does occur in several other species as well, and these are mostly taxa with large eyes. Thus, amongst the Lake Tanganyika endemics a reduced *O*A-like flange is found in *Hemibates, Trematocara, Haplotaxodon, Grammatotria, Callochromis, Xenotilapia, Cardiopharynx, Cyathopharynx* and *Aulonocara.* In contrast, *Reganochromis calliurus,* whose eye is as large as that in some *O*A species, has a moderately well-developed flange which is larger than that in any *O*A species.

The hyomandibular flange is not reduced in *Lethrinops* (Lake Malawi) nor in any of the species examined whose modal eye size (i.e. eye diameter as a proportion of head length) is less than that of any *O*A species.

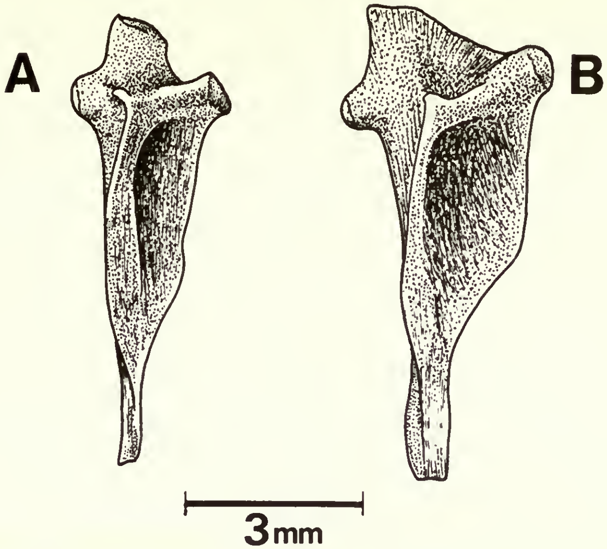

Fig. 2 Hyomandibula (right), in lateral view, of: A, *Ectodus descampsi*; B, *Astatotilapia macropsoides*.

There is thus some suggestion that a reduction in hyomandibular flange area may be correlated with a large eye size. This correlation could result, ontogenetically, from the developing eye preempting some of the space which otherwise would be available for the *levator arcus palatini* muscle whose origin is principally from the flange. It is noteworthy that in those species with a reduced flange, the *levator arcus palatini* has, relatively speaking, a reduced volume, and that its origin has shifted largely to the metapterygoid (Liem, 1981 : 195–6; personal observations).

Incidentally (*pace* Liem, 1981 : 207), in three of the four *Oreochromis niloticus* specimens examined, hyomandibular flange area is proportionately equivalent to that in the *O*A species; in the fourth specimen it is noticeably larger. The two smallest *O. niloticus* (*ca.* 42 and 52 mm standard length) have the narrowest flanges of the four specimens examined, again suggesting that flange area may be related to eye size since the smallest fishes have proportionately the largest eyes.

(3) [5] The vertical depth of the metapterygoid is shallow.

It is difficult to assess the value of this character as an indicator of phyletic relationships. The metapterygoid is noticeably shallow in all the *O*A species recognized by Liem, and in those which I would add to the assemblage. However, an equally shallow or even shallower metapterygoid is known from several Tanganyika taxa (for example, in species of *Lamprologus, Reganochromis, Trematocara, 'Limnochromis',* and also in *Perissodus hecqui, P. microlepis* and *P. eccentricus*). In some of these species the eye is large (equivalent in size to those of the *O*A species), in others it is smaller. From this information it is impossible to decide whether a shallow metapterygoid is a correlate of eye enlargement, a homoplastic feature, or one which might be indicative of phyletic relationship at a higher level than that under consideration.

(4) [2] The posterior and dorsal margins of the palatine form a 90° angle. Elsewhere, Liem (1981: 206) expands this statement and notes that 'The 90° posterodorsal angle surrounding a posterodorsal expansion of the palatine is not found in any other Tanganyika cichlids and deviates from the condition in generalized cichlids (e.g. *Astatotilapia burtoni,* Liem and Osse, 1975 and *A. elegans,* Barel, *et al.,* 1976).'

Liem (1981 : 208) places particular importance on this character, considering it as possibly the only autapomorphic feature of the assemblage.

My observations on the *O*A species indicate that the posterodorsal angle is not always rectangular and that it shows some intra- and interspecific variability. Also, I would contest the statement that the *O*A type of palatine shape is not found in other Tanganyika species. It does occur, for example, in *Limnochromis abeelei,* and is closely approached in other species as well. Furthermore it occurs in species outside the lake (e.g. *Astatotilapia macropsoides* [Lakes Edward and George] and in some *Lethrinops* species [Lake Malawi]).

I would agree, however, that the overall type of palatine morphology in *O*A species is relatively uncommon amongst African cichlids, combining as it does a straight or virtually straight posterior margin meeting the dorsal margin at, or almost at, an angle of 90°, and with a posteriorly expanded body of the bone. In combination these features give to the elongate vertical part of the bone a distinctive and near rectangular outline.

Like character (3) [5], the palatine shape is difficult to evaluate as an indicator, or potential indicator, of close phylogenetic relationship. However, since a similarly shaped bone is rarely present amongst taxa other than members of the *O*A (and in those genera where it does occur it is not manifest by all member species), and since non-*O*A taxa with this type of palatine are not closely related to the *O*A, it might well indicate a shared common ancestry for the *Ophthalmotilapia* assemblage.

(5) [4]. The anterior margin of the pterosphenoid is notched.

This character is so widely distributed amongst African cichlids (including the most generalized taxa) that it cannot be treated as an apomorphy at this level of phyletic analysis.

That the notch, or rather the tongue which delimits one aspect of the notch, has not been commented upon before, or been shown in figures of cichlid neurocrania, may well be due to its fragility and hence loss during preparation of the skull. (It is of course absent in some species and is not invariably present in all members of a genus.) Also, the process can be rather small and is then virtually invisible unless the skull is carefully cleaned of connective tissue.

Pace Liem (1981 : 207), the ligament connecting the sclerea with the pterosphenoid or its notch is present in generalized cichlids. In fact, it is present in all the cichlids I have dissected, and also in several other teleostean groups as well (including non-percoids).

(6) Liem's two myological characters, viz. [7] the *transversus dorsalis* is reduced, and [8] the *obliquus posterior* is enlarged, may be taken together.

At the outset of any discussion it must be made clear that neither character is easily assessed, partly because of insufficient comparative data from outgroups, and partly because they are not readily quantified and are thus particularly subjective.

In the discussion which follows, *Asprotilapia* is excluded from any generalizations about the *transversus dorsalis* in the *O*A; *Asprotilapia* does show unequivocally clear-cut reduction of the *transversus dorsalis anterior* and the posterior head of the muscle is not developed at all.

From my observations on dorsal gill-arch muscles in *O*A taxa, and in other cichlids from Tanganyika and elsewhere (including generalized species such as *Astatotilapia elegans,* and 'derived' taxa such as *Bathybates, Hemibates* and *Trematocara* (see also Stiassny, 1981), I would not consider the condition of the *transversus dorsalis* or the *obliquus posterior* in *O*A species to be trenchantly distinct. For example, although Liem (1981 : 207) considers the *transversus dorsalis* complex in *O*A species to be reduced relative to that in *A. elegans,* and the *obliquus posterior* to be hypertrophied, I could see no obvious differences when making the same comparisons.

That there are differences in the extent to which these and other dorsal gill-arch muscles are developed amongst African cichlids cannot be denied (see for example Liem, 1973; Liem & Osse, 1975; Stiassny, 1981). But, the differences are rarely trenchant and in some cases (including manifestly trenchant ones) are the result of environmentally induced individual variations (see Liem & Osse, 1975 : 442, fig. 11; for environmental effects, see Greenwood, 1965).

Thus, until considerably more comparative data are available, and until some means of quantifying apparent differences is employed, the use of relative muscle size would seem to be of very limited value, and could even be misleading. For those reasons I would not use either of the muscle characters in attempting to unravel the phylogeny of the *O*A (except, as noted earlier, with regard to *Asprotilapia*; see below, p. 263).

(7) [6] The operculum has a distinct auricular process.

Although Liem (1981 : 207) notes that a well-developed auricular process occurs on the operculum in several taxa, it is only in *Perissodus hecqui, 'Limnochromis' dhanisi* and the six genera now included in the *O*A (see p. 262) that I would consider the process equivalent to that found in the *O*A species. In all members of the assemblage, the opercular process, although interspecifically variable in form and size, is always a noticeable feature of the bone. That fact, coupled with the infrequent occurrence of a distinct process amongst other genera (and its mosaic interspecific distribution in those taxa), would seem to enhance its value as an indicator of monophyletic origin for the *O*A.

In brief, of the eight supposedly apomorphic characters cited by Liem as suggesting a monophyletic origin for the *O*A, only three would seem to fulfil the necessary requirements for such features, and then mainly because of their unique congruence in the species concerned. The characters, as numbered above, are: the palatopterygoid gap (1), the morphology of the palatine bone (4), and the presence of an auricular process on the posterodorsal margin of the operculum (7).

The remaining characters (i.e. 2, 3, 5 & 6) are either of no value, are possible homoplasies, or cannot be fully evaluated within the scope of our present knowledge.

There are, however, two other characters noted by Liem, and used by him at a different level of universality (the intragroup level), which I consider to be group apomorphies for the whole assemblage. These are:

(8) [15] The morphology of the lachrymal (1st infraorbital) bone.

The lachrymal in members of the *O*A has a very distinctive appearance (see Liem, 1981, fig. 5; and Figs 3A–H), one which, apparently, is not replicated in any other African cichlid. It differs from the generalized condition (as seen, for example, in *Astatotilapia macropsoides*, Fig. 3J) in its overall protraction and relative shallowness. Because the anterior portion is noticeably deeper than the posterior part, the bone has almost the appearance of a short but deep handle extending from its expanded and near rhomboidal anterior region (Figs 3A–H); although the anterior region is much deeper than the posterior part, it is by no means as expansive as it is in the majority of African cichlids.

An elongate lachrymal occurs in a few other taxa (e.g. certain *'Limnochromis'* species; Fig. 3I) but here the bone is uniformly protracted and so lacks the contrast between its shallower posterior third to half and the deeper anterior part, which is so characteristic of the *O*A type lachrymal. Also, in these non-*O*A taxa with an elongate, or relatively elongate lachrymal, the dorsal margin of the bone is but slightly concave, whereas in the *O*A species it is markedly so.

The anterior margin of the lachrymal is straight or very slightly concave, its anteroventral angle produced into a slight but distinctive peak (which is lacking in most species with an elongate lachrymal but is present in some, e.g, *'Limnochromis' permaxillaris* and *'L'. pfefferi*).

When the bone is *in situ* its anterior margin slopes upwards at an angle of 50°–60° to the horizontal (the 'modal' slope in African cichlids would seem to be one close to the horizontal, but there are several and apparently unrelated species where the slope is between 45° and 60°).

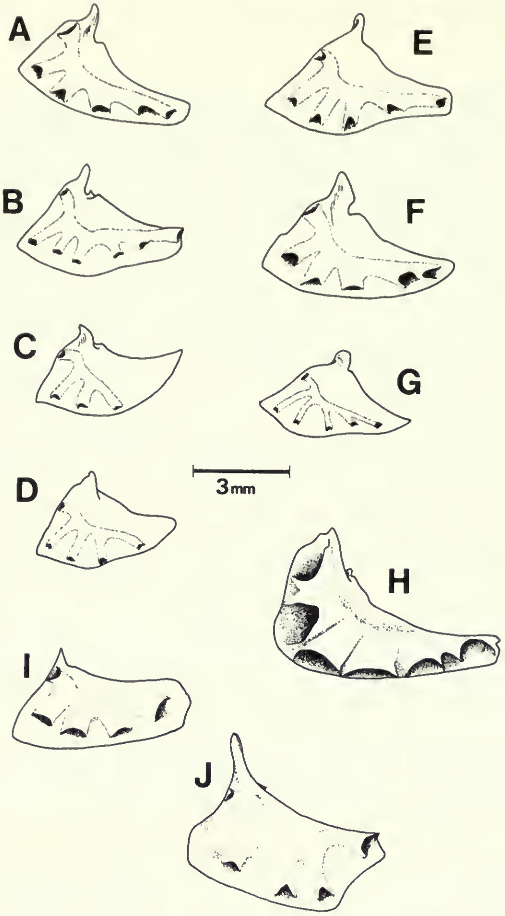

Fig. 3 Lachrymal (left), in lateral view, of: A, *Cyathopharynx furcifer*; B, *Callochromis macrops melanostigma*; C, *Xenotilapia tenuicaudata*; D, *Xenotilapia boulengeri*; E, *Grammatotria lemairei*; F, *Cyathopharynx schoutedeni* (see p. 282); G, *Asprotilapia leptura*; H, *Aulonocranus dewindti*: I, *Limnochromis auritus*; J, *Astatotilapia macropsoides*.

Liem's figure of the *O*A species *Cunningtonia longiventralis* (and his comments on the bone, Liem, 1981 : 206, fig. 5C) represents an unusual condition in that species since the anterior lachrymal margin is shown as markedly concave and aligned almost horizontally. In all 12 specimens I examined, the orientation of the bone and the shape of its anterior margin (including the anteroventral peak) are typically of the *O*A type (see Fig. 4).

There are, with very few individual exceptions, six lateral line canal pores in the lachrymal of *O*A species (but see p. 263 below). The modal number of these pores in all African cichlids is five; the occasional departure from that number seems to be attributable to individual variability. Thus, both in its outline shape (including the anteroventral peak) and in having six lateral line pores, the lachrymal appears to be a unique apomorphic feature for the *O*A.

Liem (1981 : 208) used the presence of an anteroventral peak on the lachrymal as a synapomorphy differentiating *Ectodus, Lestradea, Ophthalmotilapia* and *Cunningtonia* from *Asprotilapia* which, by implication, lacked this process. In the three specimens of *Asprotilapia leptura* (the sole species) I examined, a typical *O*A peak is present and the outline shape of the bone also conforms with that of other *O*A species (see Fig. 3G).

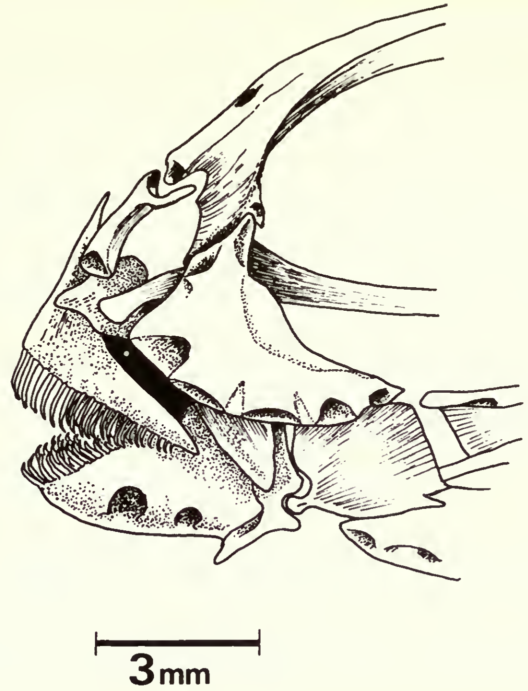

Fig. 4. *Cunningtonia longiventralis*, left lateral view of lachrymal *in situ*.

(9) [9]. The presence on the anguloarticular bone of a well-developed, anteroposteriorly aligned fossa for the insertion of the *adductor mandibulae* muscle A_2.

This well-developed fossa is noted by Liem (1981 : 195) in his anatomical description of *Ectodus descampsi*, and is illustrated in the six species depicted in his figure 4. Liem did not, however, use the feature as a major apomorphy for the *O*A as a whole. Indeed, he used the presence of an extensive fossa in *Asprotilapia* as an autapomorphic character for that genus (Liem, 1981 : 208).

In all *O*A species the fossa is clearly defined, and is limited anteriorly by a prominent, near-vertically aligned ridge on the anguloarticular. The principal surface for muscle insertion is situated on the lateral aspect of the bone, and is thus unlike the generalized condition where it lies on and across the bone's posterior margin. The insertion face, and hence the area of the fossa, varies in size amongst members of the *O*A. It is largest in *Asprotilapia,* smallest in *Cunningtonia,* with the other species occupying various intermediate positions in the range. Parenthetically, it may be noted that amongst the species I would now include in the *O*A, the fossa is small in *Cyathopharynx,* of intermediate size in *Xenotilapia* and *Grammatotria,* and largest in *Callochromis.*

Amongst the outgroup taxa examined, an *O*A type fossa is found only in *Lethrinops* (Lake Malawi), *Trematocara* (Lake Tanganyika), *Chromidotilapia batesi* and *C. kingsleyae* (West Africa) and, in a poorly developed state, in the following Lake Malawi *'Haplochromis'* species *'H.' prostoma, 'H.' johnstoni, 'H.' breviceps* and *'H.' tetrastigma.* (For the use of the name '*Haplochromis*' see Greenwood [1979 : 317]).

In all other outgroup taxa examined the *adductor mandibulae* A_2 inserts along the somewhat medially expanded posterior margin of the anguloarticular.

There is no obvious evidence to suggest a recent common ancestry shared by the *O*A and the *Chromidotilapia* species, nor one between any of the Lake Malawi *'Haplochromis'* and either the *O*A or the *Chromidotilapia* species.

In the current state of our knowledge one can be less certain about making a similar statement with respect to the *O*A and either *Trematocara* (also from Lake Tanganyika) or the Malawian genus *Lethrinops.* Thus a suspended judgement only can be given on whether the presence of an *O*A-type fossa in these three taxa is a homoplasy, or whether it is a synapomorphy for a group of higher universality than the one under discussion (see also p. 257).

Because the fossa is present in all *O*A species (including the new additions, see below) and because it is congruent with other apomorphic features shared by them, it can, I would consider, be taken as further evidence for the monophyly of the lineage.

To summarise this review of group characters in the *Ophthalmotilapia* assemblage (as defined by Liem, 1981), the congruent apomorphic features are:

(i) The presence of a palatopterygoid gap (see p. 254)
(ii) The morphology of the palatine bone (see p. 257)
(iii) The presence of an auricular process on the opercular bone (see p. 259)
(iv) The shape of the lachrymal bone (1st infraorbital); see p. 259)
(v) The presence of a well-defined, laterally placed fossa for the insertion of the A_2 *adductor mandibulae* muscle on the anguloarticular bone (see p. 261).

The *Ophthalmotilapia* assemblage reconsidered

On the grounds of all their constituent species sharing the five features listed above, and because none possesses any feature which might suggest other relationships, six further genera can be included in the *Ophthalmotilapia* assemblage (see Figs 1, 3, 10 and 11).

The new additions are:

(i) *Xenotilapia* Blgr, 1899 (type species *X. sima* Blgr)
(ii) *Callochromis* Regan, 1920 (type species *Pelmatochromis macrops* Blgr)
(iii) *Grammatotria* Blgr, 1899 (type species *G. lemairii* Blgr)
(iv) *Cyathopharynx* Regan, 1920 (type species *Tilapia grandoculis* Blgr; but see p. 284).
(v) *Cardiopharynx* Poll, 1942 (type species *C. schoutedeni* Poll)
(vi) *Aulonocranus* Regan, 1920 (type species *Paratilapia dewindti* Blgr)

Although not apparently relevant to the question of their phyletic relationships, it may be noted that these six genera also share with members of Liem's original *O*A all the other features discussed in the previous section (i.e. characters 2, 3, 5 & 6).

For taxonomic and biological details of these genera and their contained species, reference should be made to Poll (1946 & 1956). Since I can find no grounds for maintaining *Cyathopharynx* and *Cardiopharynx* as separate genera (see p. 282), all further references to these taxa will be made under the name of the senior synonym, *Cyathopharynx.*

Liem (1981 : 208) has already suggested that *Xenotilapia, Callochromis* and *Aulonocranus* might be the sister lineage of the *Ophthalmotilapia* assemblage, but he felt that more information was needed before their 'precise relationships' to the others could be determined. His reason for making this suggestion was that all three genera share with the *O*A a palatopterygoid gap and various derived features of the hyomandibula, *ie* characters (1) and (2) above. That the three taxa also shared the other six and supposedly apomorphic features originally used to define the *O*A, was not noted by him.

Although I would be chary of claiming that the 'precise relationships' of *Xenotilapia, Callochromis, Aulonocranus, Grammatotria* and *Cyathopharynx* have been determined, I would submit that an *a priori* case can be established for including them within the *Ophthalmotilapia* assemblage itself, and not just as a sister-group to that lineage.

Before going on to consider intralineage relationships within the expanded *O*A, some comments must be made about certain features in *Aulonocranus* and *Xenotilapia.*

In *Aulonocranus* the lachrymal has the characteristic shape of that bone in other *O*A species (Fig. 3H), but it lacks the anteroventral peak; the anteroventral angle is rounded and so resembles the condition found in most cichlid taxa. It is possible that this atypical anterior profile might be attributed to the greatly inflated laterosensory canals in the lachrymal of *Aulonocranus*.

In most *Xenotilapia* species too, the lachrymal is atypical for the *O*A because in these species there are, modally, five and not six openings to the laterosensory canal system (Figs 3C & D). There is, however, considerable inter- and intraspecific variation in pore number; some species have six pores, others only four, and some individuals have a different number of pores on each side of the head. Clearly, pore number is an unstable characteristic in *Xenotilapia*. The genus also differs from all other *O*A taxa, and all other African cichlids I have examined, in having the posterior opening to the lachrymal laterosensory system positioned below and not opposite the anterior canal opening in the second infraorbital bone.

As in *Aulonocranus*, the outline shape of the lachrymal in *Xenotilapia* is a typical *O*A one (Figs 3C & D); not surprisingly, considering the number of species (11), there is rather more variation on that basic shape in *Xenotilapia* than in other members of the assemblage.

Relationships within the *Ophthalmotilapia* assemblage

In its original form, the assemblage was divided into two major sublineages, one comprising only *Asprotilapia leptura*, the other containing the four remaining genera, *Ectodus, Lestradea, Ophthalmotilapia* and *Cunningtonia* (see Liem, 1981 : 208 & fig. 9).

As defining features for the larger sublineage, Liem employed two supposedly synapomorphic characters: (i) the morphology of the lachrymal, and (ii), the dominance of the A_1 division of the *adductor mandibulae* muscle complex (Liem's characters 15 & 16 respectively).

The *Asprotilapia* lineage was recognized both by the absence of those features, and, more importantly, by its having six presumed autapomorphic characters (see Liem, 1981 : 208).

As argued above (character (8)[15], page 259), the features of the lachrymal must now be considered an apomorphic character for the whole *O*A (including the new additions and *Asprotilapia* itself).

The muscle character, according to Liem, has two components. First, that the A_1 division of the *adductor mandibulae* has become the dominant component of the complex, its cross sectional area surpassing '. . . that of the other parts', and second, that '. . . its origin has expanded ventrally at the expense of the adductor mandibulae part A_2' (Liem, 1981 : 208).

It is difficult to test the first claim adequately, and my attempts to do so failed to confirm Liem's claims, especially if, as his statement implies, the A_1 division is dominant to both the A_2 and A_3 divisions combined. However, the area of origin of A_1 in the taxon concerned is very clearly greater than that of A_2 when measured by its extent along the vertical arm of the preoperculum (see fig. 6 in Liem, 1981).

When, however, the additional *O*A taxa are taken into account, the second feature shows a continuous range of variation from a state where the origins of both A_1 and A_2 occupy an approximately equal depth on the vertical preopercular limb, to one where the origin of A_2 is virtually excluded from that limb and thereby is almost confined to the horizontal part of the bone. Furthermore, even within a single genus (as in *Xenotilapia* and *Callochromis*) some species have A_1 and A_2 with almost equal depths of vertical origin (the plesiomorph condition in cichlids), others have the depth of A_1 greater than A_2, and yet others have A_2 with a much greater vertical depth of origin than A_1 (Fig. 5B). Thus there would no longer seem to be any grounds for maintaining the unity of the *Ectodus-Cunningtonia* sublineage on the basis of its myological characters.

The peculiar arrangement of the *adductor mandibulae* muscles in *Asprotilapia* still stands as a well-defined autapomorphy for the genus. Here, division A_1 is markedly reduced, both in the depth of its origin on the preoperculum, and in its overall bulk (Fig. 5A), a condition not found elsewhere in the *O*A. Other features, however, suggest that *Asprotilapia* is closely related to some of the newly incorporated members of the assemblage (p. 265).

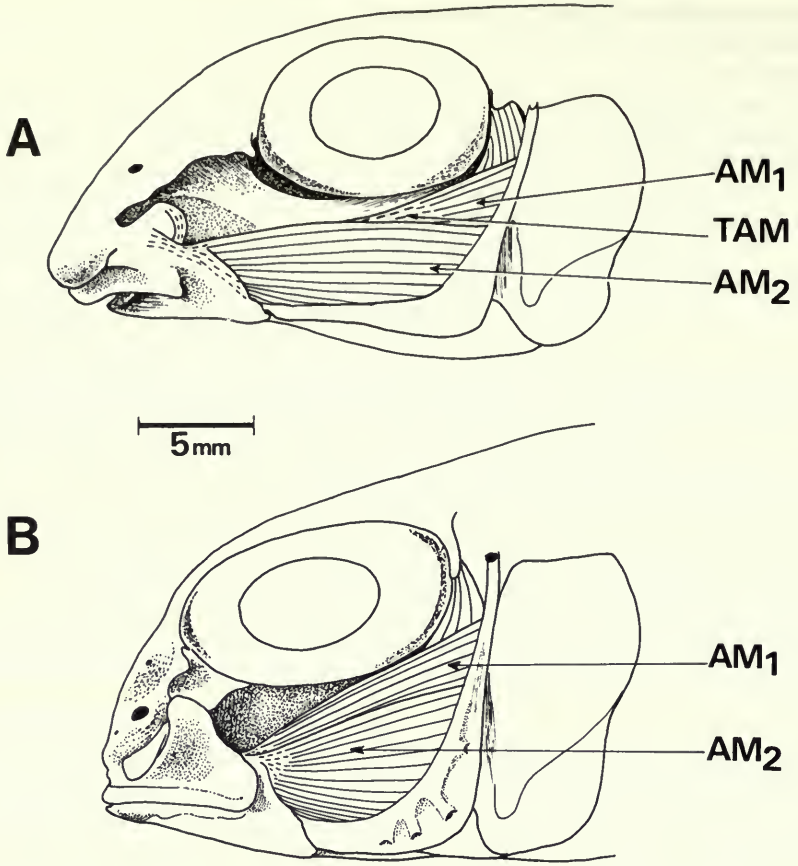

Fig. 5 Superficial *adductor mandibulae* muscles (left side) of: A, *Asprotilapia leptura*; B, *Xenotilapia sima*. AM$_1$ & AM$_2$: *adductor mandibulae* divisions 1 and 2; TAM$_1$: tendon of insertion for AM$_1$.

Although a primary dichotomy within the *O*A cannot be made on the characters employed by Liem, such a dichotomy can be established on differences in the length of the gut and the manner in which it is arranged within the visceral cavity (see Figs 6 & 7).

Liem (1981 : 209; character [19]) used intestinal length to define a group of taxa (*Ophthalmotilapia, Cunningtonia* and *Lestradea*) within the original *O*A, but he did not comment on the spatial arrangement of the alimentary tract in those species.

Within the expanded *O*A, the member taxa can be grouped into those with an intestinal length less than 3 times the standard length of the body, modally 2·3–2·5 times SL, and those with an intestinal length 3–6 times the standard length.

Species in the first group have the relatively short gut coiled into a few loops whose arrangement is in an essentially anteroposterior direction. In contrast, species with a long gut have the intestine much coiled and the coils are arranged in an essentially transverse direction (see Figs 6 & 7). At first sight this transverse arrangement gives an erroneous impression of the intestine actually being coiled around the stomach (Fig. 7).

A long and complexly coiled gut is a derived feature, occurring in several cichlid lineages. But, since these lineages are not closely related it can be treated as a synapomorphy at the level of universality involved here.

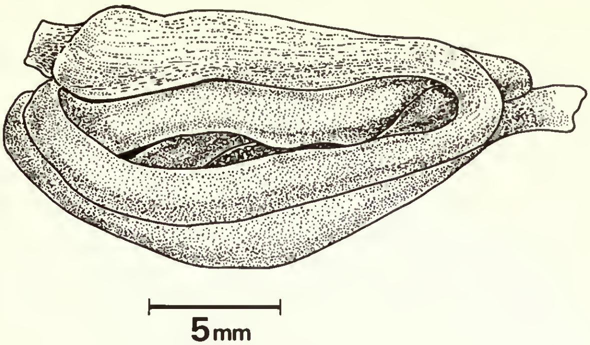

Fig. 6 Alimentary tract (left lateral view) of an *Asprotilapia* subassemblage taxon (*Grammatotria lemairei*).

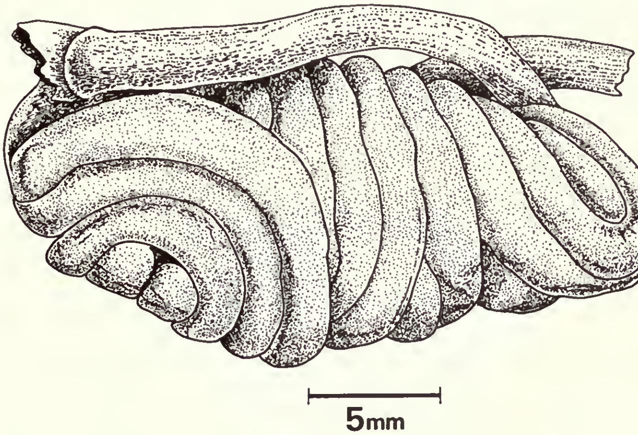

Fig. 7 Alimentary tract (left lateral view) of an *Ophthalmotilapia* subassemblage taxon (*Ophthalmotilapia boops*).

Taxa of the *O*A belonging to the group with a long and transversely coiled intestine are: *Lestradea, Ophthalmotilapia, Cunningtonia* and *Cyathopharynx* – hereafter referred to as the *Ophthalmotilapia* subassemblage; their interrelationships will be considered later (see p. 271).

The group with a short and longitudinally coiled intestine comprises the genera *Asprotilapia, Callochromis, Xenotilapia, Grammatotria, Ectodus* and *Aulonocara* – hereafter referred to as the *Asprotilapia* subassemblage.

Four genera in the *Asprotilapia* subassemblage, viz. *Asprotilapia, Callochromis, Xenotilapia* and *Grammatotria,* share an apomorphic feature which suggests their shared common ancestry. This character is the presence of a fully developed pharyngeal hanging pad, with its associated modifications to the superficial anatomy of the gill-rakers; see Figs 8 & 9.

The pad is an hypertrophied and well-circumscribed, forwardly directed, and turgid fold of the buccopharyngeal tissues. It lies immediately anterior to the upper pharyngeal bones and extends forward and downward, as a visor-like projection, for a short distance in front of the first gill-arch. Posterolaterally the pad is fused with the thickened tissue covering the epibranchial gill-rakers of the first gill-arch, but over most of its width the visor-like part is

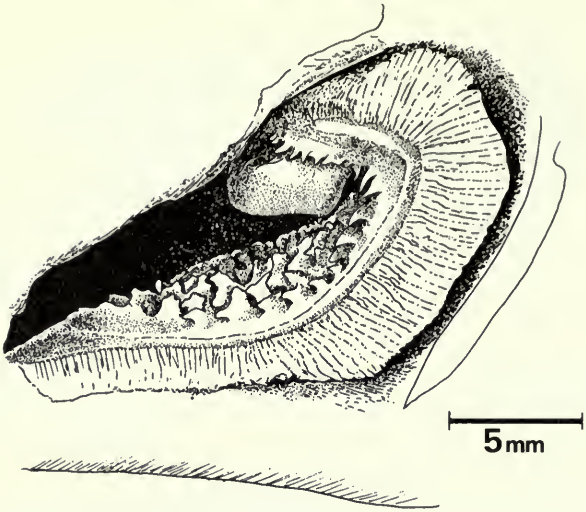

Fig. 8 Pharyngeal hanging pad in *Xenotilapia boulengeri.* Left side, seen from a slightly dorsolateral viewpoint.

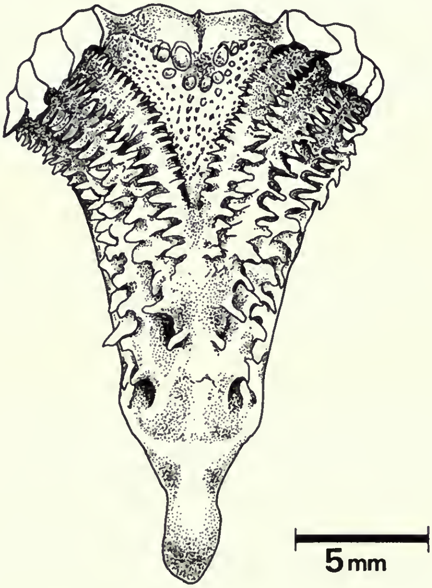

Fig. 9 Ventral portions of the gill-arches, and the lower pharyngeal bone of *Xenotilapia boulengeri,* viewed from above to show the nature of the gill-rakers.

separated from the buccal roof by a distinct transverse groove. This groove is open anteriorly and laterally. In the buccal midline the left and right halves of the visor-like portion are confluent with the buccopharyngeal roof. When the mouth is closed, and the ventral gill-arch skeleton is adducted, the visor occludes the pharynx, leaving only a narrow channel coincident with the medial area of confluence between the two halves of the visor and the buccopharyngeal epithelium.

The pharyngeal surface of the visor is thrown into a large number of broad-based but terminally acute papillae. When the gill-arches are adducted the papillose area is brought into close contact with the upper surface of the cerato- and hypobranchial regions of the gill-arches. These, in turn, are covered by a greatly thickened and soft epithelium. The inner and outer gill-rakers on the ceratobranchial of each arch are joined transversely by anvil-shaped folds of thickened tissue so that, superficially, there appears to be but a single series of rakers, with each raker extending across the breadth of the arch (Fig. 9).

A pharyngeal hanging pad is known from two other, and very dissimilar, African genera, *Chromidotilapia* and *Tylochromis,* and in the South American *Geophagus* (see Trewavas, 1974 : 389–392). Since there are several features strongly indicating that none of these taxa is closely interrelated, and that none is closely related to the *Ophthalmotilapia* assemblage, the repeated occurrence of a hanging pad can only be interpreted as the result of convergent evolution. Any other explanation would be most unparsimonious. It would be equally unparsimonious to assume that its occurrence in four of the *O*A taxa was the result of independent evolution in each genus. This is particularly so since three of the four genera share another apomorphy, a high number of caudal vertebrae in *Xenotilapia, Asprotilapia* and *Grammatotria*, and a second derived character, the shape of the dentary, is shared by *Xenotilapia, Callochromis* and *Grammatotria*, of which taxa *Callochromis* alone does not share the vertebral apomorphy.

Thus, on the basis of their all possessing a pharyngeal hanging pad, *Xenotilapia, Callochromis, Grammatotria* and *Asprotilapia*[1] are taken to form a natural group within the *O*A. The group can be further subdivided on the distribution within its members of certain other derived features.

Xenotilapia, Callochromis and *Grammatotria* all have a peculiarly shaped dentary (Fig. 10). When viewed laterally, the dorsal margin of the bone is seen to dip downwards immediately behind the last tooth in the outer row. It continues posteriorly at this lower level until it curves upwards to form the anterior margin of the coronoid process. The alveolar surface is confined to that part of the bone preceding the step, behind which it is edentulous. The dentary of *Asprotilapia* will be discussed below.

This type of dentary, as far as I am aware, is not found in any other cichlid from Lake Tanganyika, or for that matter from Lake Victoria either. It is, however, closely approached by the dentary in the Malawian genus *Lethrinops* and in some *'Haplochromis'* species from that lake. The significance of this similarity, and the occurrence in *Lethrinops* of a palatopterygoid gap, is discussed on page 279.

Within the group comprising *Xenotilapia, Callochromis* and *Grammatotria* it is impossible to determine which two genera are the more closely related since no clear-cut linking synapomorphies can be recognized. It is accepted that the diagnostic 'generic' characters for each genus are autapomorphies for that taxon. At present the trio can only be treated as an unresolved trichotomy, but with the suggestion that further research may show *Xenotilapia* and *Grammatotria* to be sister taxa.

Asprotilapia, the fourth member of the group, is a most distinctive taxon, in which Liem (1981 : 208) identified six autapomorphies. These must now be reviewed in the context of the expanded *Ophthalmotilapia* assemblage.

As in earlier discussions, Liem's apomorphy number is given in square brackets.

> (i) [9]. The elongate, slender mandible has an expanded adductor fossa for the A_2 division of the *adductor mandibulae* muscle.

As noted earlier (p. 261) the adductor fossa is expanded in several members of the *O*A, particularly in species of the group to which *Asprotilapia* belongs. However, even amongst those species the fossa is most expansive in *Asprotilapia.*

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[1] Microbranchiospines are present in all four of these Tanganyika genera; in this respect they resemble *Tylochromis* and differ from *Chromidotilapia* (see discussion in Trewavas, 1973 : 17 & 1974 : 388).

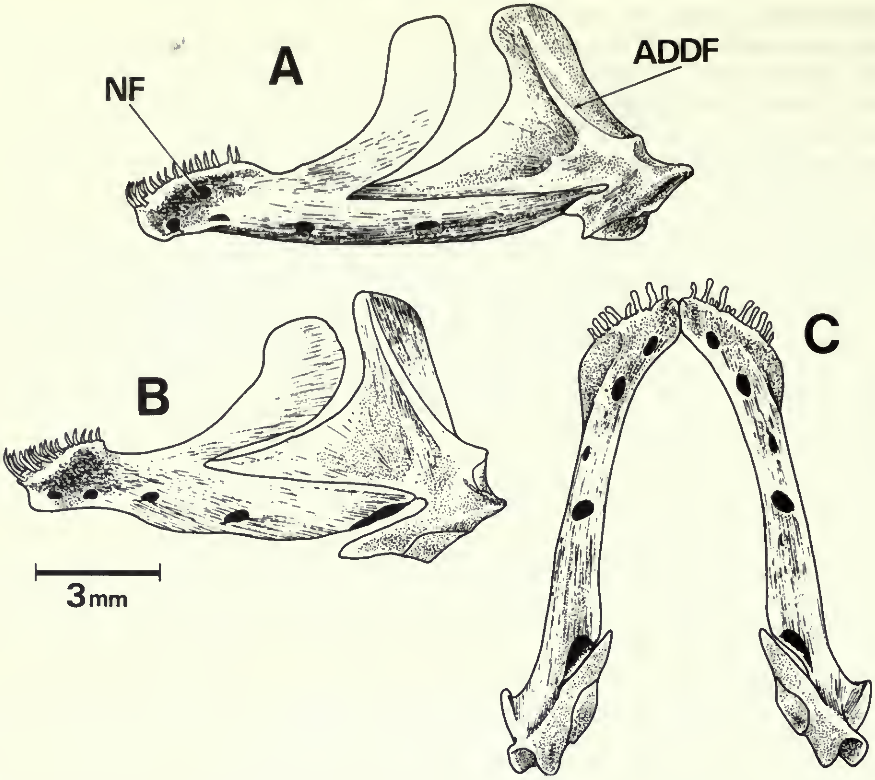

Fig. 10 Dentary and anguloarticular in two species of the *Asprotilapia* subassemblage: A, *Grammatotria lemairei* (lateral view); B & C, *Xenotilapia boulengeri* (lateral and ventral views respectively). ADDF : adductor fossa. NF : nerve foramen.

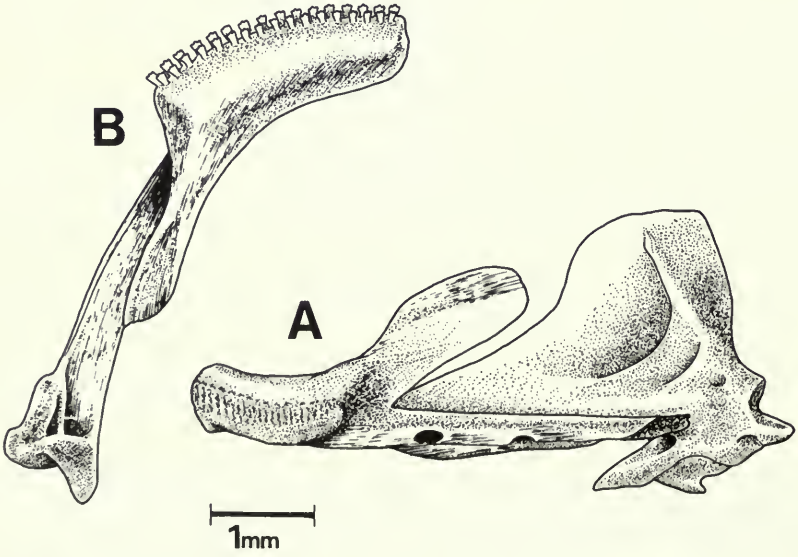

Fig. 11 Left dentary and anguloarticular of *Asprotilapia leptura* in : A, lateral view; B, occlusal view. In B the teeth have been restored (based on a spirit specimen), but in A only the tooth scars are shown.

The mandible is not, in my view, especially elongate, particularly when it is compared with that element in other members of the *Asprotilapia* subassemblage (cf. Figs 10 & 11). Its gross morphology differs from that in *Xenotilapia, Callochromis* and *Grammatotria* since it lacks a 'stepped' alveolar margin, and because each ramus of the jaw has a more abrupt and stronger medial curvature towards the symphysis. Also, in *Asprotilapia,* immediately before the dentary curves inwards, the alveolar surface is produced laterally so as to form a noticeable, shelf-like overhang of the underlying ramus (Fig. 11).

Overall, the dentary in *Asprotilapia* bears a fairly close resemblance to that bone in *Labeotropheus* of Lake Malawi, a resemblance enhanced by the tricuspid, slender-necked, procumbent and movably implanted teeth present in both genera. *Asprotilapia* has, however, a shallower dentary, and the anguloarticular is taller and more expansive than in *Labeotropheus.* Parenthetically it may be noted that *Asprotilapia,* like *Labeotropheus,* has an enlarged and similarly shaped cartilaginous meniscus underlying the premaxillary ascending process, and a similar fleshy medial projection overlying the broad palato-premaxillary ligaments. Observations made from radiographs of the two species, and from manipulation of preserved specimens, indicate that the protrusile mechanisms in the two species are very similar. There are, however, no reasons to doubt that these similarities should be treated as homoplasies.

(ii) [10]. The posterior head of the *transversus dorsalis anterior* muscle is absent.

This seems to be a clear-cut autapomorphy, but should be checked in more examples than the single specimen available to Liem and myself.

(iii) [11]. Lateral ethmoids greatly enlarged.

This again is an apparently good autapomorphy.

(iv) [12]. Interorbital width greatly reduced.

The interorbital width is reduced in some *Xenotilapia* species, but in none is it as narrow as in *Asprotilapia.*

(v) [13]. The reduced articular process of the premaxilla is in a more forward position.

There is considerable and continuous variation in the relative position of this process in *Xenotilapia* species, and indeed within the taxa of the entire *O*A. It would not, therefore, seem to be a character of particular value.

(vi) [14]. The greatly enlarged cranial condyle and the premaxillary process constitute the bulk of the maxilla.

The maxilla of *Asprotilapia* is less outstanding when compared with that bone in other members of the subassemblage, especially *Xenotilapia* (Fig. 12). In *X. boulengeri,* for example, the process is larger than in *Asprotilapia.* The cranial condyle, however, is largest in *Asprotilapia* and, as compared with all other *O*A species, the whole bone is relatively foreshortened.

In the context of the expanded *O*A, I would consider that at least three of the autapomorphies originally proposed (i.e. nos. i, ii and iii above) retain their validity (if, that is, the apomorphic features of the lower jaw are interpreted as has been done here).

Although not listed as an autapomorphy by Liem (1981), the peculiar condition of the A_1 division of the *adductor mandibulae* muscle in *Asprotilapia* would seem deserving of that status. In *Asprotilapia,* as compared with all other *O*A taxa, A_1 is a very short and narrow muscle with an extremely long tendon of insertion (Liem, 1981; fig. 6; also Fig. 5), and an area of origin much smaller in all respects than that of the A_2 division. No other species in the *O*A has this arrangement of the *adductor mandibulae* muscles.

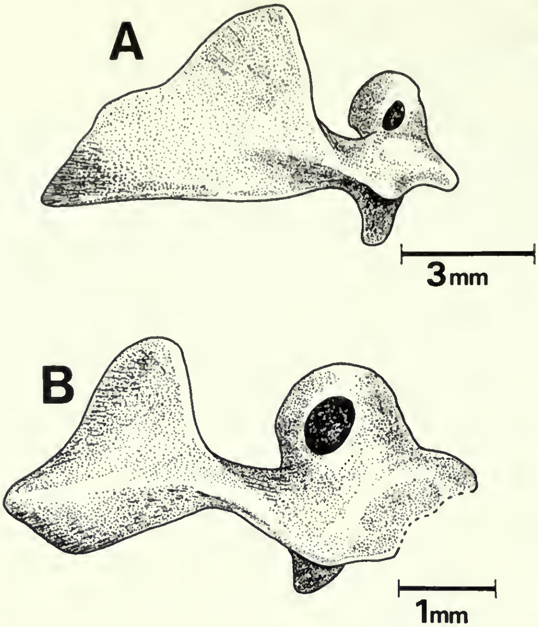

Fig. 12 Right maxilla, in lateral view, of: A, *Xenotilapia boulengeri*; B, *Asprotilapia leptura* (the damaged ventral margin of the premaxillary saddle is indicated by a broken line).

When commenting on the unusual A_1 muscle in *Asprotilapia,* Liem (1981 : 203) makes particular reference to a tendon stemming from the muscle's principal tendon of insertion, and which joins the tendinous part of adductor division A_ω. This emphasis might give an impression that the vertically directed interconnecting tendon is a unique (or unusual) feature of *Asprotilapia.* That is not so because the tendon is present in all cichlids whose jaw musculature has been examined (see for example Liem & Osse, 1975: fig. 6; Stiassny, 1981 : 80, and figs 8 & 11 [tA_1b]; also personal observations on species other than those studied by these authors). *Asprotilapia* is, however, unusual in having a discrete, ligament-like condensation in the connective tissue between the premaxilla and dentary, inserting on the lateral (and not the medial) face of the premaxilla.

Interestingly, despite the resemblances in lower jaw morphology between *Asprotilapia* and *Labeotropheus* (see above p. 269), the pattern of adductor muscles in the two genera is quite different. *Labeotropheus* has the typical generalized cichlid arrangement.

The various autapomorphies of *Asprotilapia* serve to indicate the taxon's isolation within its group. For the moment it can only be treated as the sister taxon to the other three genera (i.e. *Callochromis, Xenotilapia* and *Grammatotria)* combined.

The two remaining taxa in the *Asprotilapia* subassemblage (see p. 265), *Ectodus* and *Aulonocranus,* are 'interrelated' only at the level of their sharing with their supposed sister-group, *Asprotilapia, Callochromis, Xenotilapia* and *Grammatotria,* the plesiomorphic feature of a short intestine. With one possible exception, neither *Ectodus* nor *Aulonocranus* has any uniquely shared derived features suggestive of their recent common ancestry.

The exceptional feature concerns the marked elongation of the first, and to a lesser extent the second pelvic fin rays in adult males. In *Aulonocranus* the first ray extends to about the middle of the anal fin, and in *Ectodus* to a point beyond its spinous part, but never as far as the middle of the fin. Other members of the *Asprotilapia* subassemblage have variously modified relative proportions of different pelvic fin rays (see Poll, 1956) but none has the first ray elongated to the degree found in *Ectodus* and *Aulonocranus.* The significance of this feature is, however, somewhat questionable (see p. 272).

In Liem's scheme (1981 : 208–9, fig. 9), *Ectodus* was allied with *Lestradea, Ophthalmotilapia* and *Cunningtonia* (now considered to be a separate sublineage, see below) and not with *Asprotilapia.* Liem's grounds for this alliance were based on *Ectodus* sharing two apomorphic characters with *Lestradea, Ophthalmotilapia* and *Cunningtonia,* namely a distinct antroventral process on the lachrymal bone, and a dominant A_1 division in the *adductor mandibulae* muscle complex.

As was argued above (pp. 262–263) the former character is one shared by all members of the *O*A (except *Aulonocranus*) and the latter is a variable feature of little value as an indicator of relationships within the *O*A.

Aulonocranus was not included in the original *O*A, although Liem (1981 : 206 & 208) did suggest that it might be related to that assemblage.

The genus is readily identified by one outstanding apomorphy, the hypertrophy of its cephalic laterosensory canal system, and as a probable correlate, the enlarged saccular bulla in the basioccipital and prootic bones.

Ectodus has one autapomorphy, viz. the vertical and horizontal limbs of the preoperculum are of equal or almost equal length (see Liem, 1981 : 209). Liem also ranked the enlarged saccular bulla as an autapomorphy, but the bulla is enlarged to an equal extent in *Lestradea* and *Ophthalmotilapia* amongst members of the original *O*A, and in *Aulonocranus* and *Cyathopharynx* among the new additions to the assemblage. Indeed, apart from *Callochromis, Xenotilapia* and *Grammatotria* the saccular bulla is noticeably enlarged in all *O*A species, the degree of enlargement showing a continuous increase from the condition in *Asprotilapia* through to that in *Aulonocranus,* with *Lestradea, Ectodus* and *Ophthalmotilapia* all close to *Aulonocranus.*

Turning now to the second lineage of the primary dichotomy, the *Ophthalmotilapia* subassemblage (p. 265), one again finds difficulty in establishing intragroup relationships, but little difficulty in recognizing autapomorphies for the constituent genera, viz. *Lestradea, Ophthalmotilapia, Cunningtonia* and *Cyathopharynx.*

Since *Lestradea* lacks the various derived features shown by its congeners in the subassemblage it would appear to be the plesiomorph sister taxon to the other three genera combined.

Liem (1981 : 209) singled out two autapomorphies for *Lestradea* (i) the edentulous anterior process of the lower pharyngeal bone is only half as long as the toothed part (his apomorphy 20), and (ii), the body of the maxilla is stout, and has a prominent postmaxillary process (his apomorphy 21).

I cannot agree with Liem's statement about the relative proportions of the anterior process of the lower pharyngeal bone. The *Lestradea* specimens I have examined all have this process as long as, or almost as long as the toothed part, a condition approaching that in *Ophthalmotilapia* and *Cunningtonia.* This condition must be considered derived relative to that in *Astatotilapia* and many other African cichlids. In these various taxa the edentulous anterior process of the bone is indeed half or less than half as long as the toothed part.

The body of the maxilla in *Lestradea* is stout and the posterior process is prominent, but in both features the bone does not differ from the maxilla in *Ophthalmotilapia* where the process is a little less prominent. A relatively short maxilla with a prominent posterior process is, it would seem, a common feature in the whole *Ophthalmotilapia* assemblage.

Cyathopharynx is readily distinguished by its autapomorphous lower pharyngeal bone (Fig. 23), with its deeply concave occlusal surface, heart-shaped dentigerous area, and greatly inflated body below that surface. There are, however, no synapomorphies (except group ones) shared by *Cyathopharynx* and any other member of the subassemblage.

Liem (1981 : 209) recognized three synapomorphies which suggested to him that *Ophthalmotilapia* and *Cunningtonia* were members of a monophyletic unit. The presumed synapomorphies were (i) jaw teeth with long stalks, and movably implanted, (ii) the first pelvic ray greatly elongate (Liem's apomorphies 22 & 23 respectively), and (iii) the posterior margin of the vertical preopercular limb is straight and forms a 90° angle with the horizontal limb.

The teeth in all members of the *O*A (*sensu lato*) are movably implanted, and in all species the teeth could be described as having 'long stalks', albeit with specifically distinct but varying degrees of slenderness. For example, in both these features the outer jaw teeth in *Ophthalmotilapia* are very like those in *Lestradea*, but those in *Cunningtonia* have a much more slender and elongate neck than do the teeth in any other *O*A species.

The first and second pelvic rays are elongate (much more so in males than in females) in both *Ophthalmotilapia* and *Cunningtonia,* with, in the former, the first ray somewhat longer than the second. But, when other species in the expanded *O*A are taken into account one finds that the condition of the two rays in *Cyathopharynx furcifer* is like that in *Cunningtonia longiventralis,* and that *Aulonocranus* also has elongate rays but which extend only to the middle of the anal fin base and not to the posterior margin, or slightly beyond, as they do in *Cunningtonia* and *Cyathopharynx furcifer. Cyathopharynx schoutedeni* has elongate first and second pelvic rays too, but in this species it is the second ray which is the longer and, unlike the elongate first ray in *C. furcifer,* it extends posteriorly only a short distance beyond the spinous part of the anal fin.

Thus it is difficult to treat marked elongation of the first, or first and second pelvic rays as a synapomorphy for *Ophthalmotilapia* and *Cunningtonia.* That it is a character showing continuous variation and one that is incongruent with other apomorphies would also preclude its use as an indicator of recent shared common ancestry for the genera exhibiting it, namely *Aulonocranus, Ophthalmotilapia, Cunningtonia* and *Cardiopharynx* (see below).

Some comment on the spatulate, bifid tips to the first ray in males of *Ophthalmotilapia* species would be appropriate here.

The feature appears to be a unique apomorphy for *Ophthalmotilapia,* indeed it is one of the reasons given by Liem (1981 : 210) for synonymizing *Ophthalmochromis* with that genus. Spatulate tips have not been mentioned in the formal descriptions of any other species, nor have I seen such modifications in any of the taxa, other than *Ophthalmotilapia,* which I have examined. However, Brichard (1978 : 187) describes the pelvic fin in *Cyathopharynx furcifer* as having '. . . a long filament tipped with a yellow double spatula'. On page 190 of the same book he comments on 'The ventral filaments, reaching the end of the anal fin are each tipped with a double yellow-orange spatula'. Finally, Brichard (1978 : 148 & 149) provides two illustrations of a live individual (or individuals) showing what certainly looks like a spatulate tip to the protracted pelvic fin rays.

Brichard is an experienced underwater-naturalist and one is hesitant to suggest he has misidentified his material. On the other hand, in his description (Brichard, 1978 : 326) of *Ophthalmotilapia ventralis* (as *Ophthalmochromis ventralis*) he remarks that 'The males . . . have very long pelvic filaments also forked like *O. nasutus,* but the tips are **without spatulae** (although they are pale yellow like those of *O. nasutus*)'; bold type added. Clearly there is some terminological confusion here since none of the male *O. ventralis* specimens I have examined, or those which have been described elsewhere, lacks well-defined spatulae.

The tips of the elongate pelvic rays in *Cyathopharynx* are brightly coloured, and seem to serve the same ethological function as the spatulae in *Ophthalmotilapia.* Perhaps the confusion stems from that colour similarity rather than a structural one? Until spatulate *Cyanopharynx* are described formally, the uncertainty will remain.

In itself, very marked elongation of the first and second pelvic rays is a derived feature (see below), but in the context of the *O*A it is not clear at what level of universality it can be recognized as a synapomorphy. For example, if used to unite *Aulonocranus, Cyathopharynx, Ophthalmotilapia* and *Cunningtonia,* pelvic fin length would be incongruent with the group synapomorphy of an elongate and complexly folded intestine shared by all except *Aulonocranus,* which has a short and simply folded intestine. If, on the other hand, because of its short gut *Aulonocranus* was taken to be the plesiomorph sister taxon of the others, then where would *Lestradea* which has a long gut but short pelvic fins be placed?

The problem is further compounded by *Ectodus* which has a short and simply folded gut but elongate first and second pelvic rays produced to a degree almost comparabale with those in *Aulonocranus.*

In no case are there any known synapomorphies which are uniquely congruent with protracted pelvic fin length, and which would thereby establish a strong case for arguing that the gut character is a homoplasy. Finally, it must be recalled that some relative elongation of the first and second pelvic rays is of relatively common occurrence in African cichlids (see Greenwood, 1981), and that the degree of elongation must be treated as a continuous variable, albeit one rarely reaching the extremes found in *Cunningtonia* and *Ophthalmotilapia.*

Liem's third synapomorphy (involving the shape of the preoperculum; see page 271) is also difficult to substantiate, particularly in the context of the expanded *O*A. In all constituent species of the *O*A *sensu lato* the vertical and horizontal limbs of the preopercular bone meet at, or very nearly at, a right angle, and in all except *Ophthalmotilapia* and *Cunningtonia* the posterior margin of the vertical limb curves inwards for a short distance near its dorsal extremity. Because *Ophthalmotilapia* and *Cunningtonia* have the bony flange behind the vertically aligned laterosensory canal tube narrowing imperceptibly, rather than abruptly, the entire posterior margin of the preoperculum does give the impression of being straight in these two species. The difference between the two types of posterior margin is, however, very slight and is almost obliterated by the condition in *Cyathopharynx.* Here the dorsal extremity of the margin is slightly indented, but less noticeably so than in most other *O*A taxa.

Thus, of the three apomorphies under review, only the nature of the preopercular margin, a not particularly trenchant character, would seem to be a synapomorphy linking *Ophthalmotilapia* and *Cunningtonia.*

On the morphological evidence alone, it is thus impossible to hypothesize precise intragroup relationships for the *Ophthalmotilapia* subassemblage, except to note that on a simple summation of derived features *Lestradea* would seem to be the most plesiomorph taxon. At the generic level the other taxa are readily identified by their particular autapomorphies (see below).

It is possible that these currently obscure and therefore uncertain intralineage relationships will be clarified when more data are available on the breeding habits of its constituent species. Brichard (1978 : 108), for example, groups *Cyathopharynx* with *Ophthalmotilapia* as polygamous spawners in which there is no contact between the sexes at the nest site. The import of Brichard's statement is not really clear, and the phyletic importance of most ethological characters still awaits evaluation. Nevertheless it is suggestive that Brichard did single out these taxa as forming a distinctive reproductive class.

Returning now to the autapomorphic features of the genera constituting the subassemblage, one finds that *Ophthalmotilapia* (*sensu* Liem, 1981 : 210) is distinguished by the bifid spatulae in which each elongate first pelvic ray terminates, and the subdivision of the *retractor dorsalis* muscle of the upper gill-arches into two distinct heads (see Liem, 1981 : 201, fig. 8D).

Cunningtonia has as its principal autapomorphies the nature of its oral dentition, the stout foreshortened dentary (Fig. 13) and the stout premaxilla.

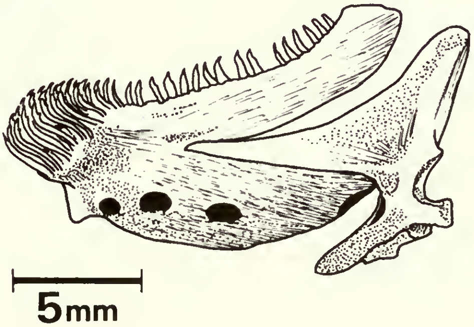

Fig. 13 Left dentary and anguloarticular of *Cunningtonia longiventralis* in lateral view.

Most of the jaw teeth are very slender and tall, with strongly recurved, tricuspid and broad crowns. The teeth are arranged in wide bands over the entire alveolar surface of the premaxilla and on the transverse part of the dentary, but on the lateral alveolar surface the teeth are much stouter and are unicuspid.

The palatine of *Cunningtonia* is also unique in having its facet for articulation with the lateral ethmoid expanded medially into a shelf-like projection. When viewed from the side, especially in specimens prepared as alizarin transparencies, the shelf has a spine-like appearance (see Liem, 1981 : 210; apomorphy 26).

Liem considered that the symplectic in *Cunningtonia* was '... very elongate' (his apomorphy 28), but I find that it is of virtually equal relative length in all members of the *O*A.

In *Cyathopharynx* the principal autapomorphy is the peculiar, heart-shaped and deeply concave dentigerous surface of the lower pharyngeal bone and, of course, the correlated changes in the shape of the upper pharyngeal elements (see p. 288).

The nature of the apophysis for the upper pharyngeal bones in the *Ophthalmotilapia* assemblage

Like Liem (1981), I have not taken into account the nature of the pharyngeal apophysis when analysing intragroup relationships amongst members of the *O*A (see Greenwood, 1978, for an evaluation of this character in determining phyletic relationships; also Fryer & Iles, 1972 : 504 *et seq.*).

Based on material examined personally, the distribution of apophyseal types (defined as in Greenwood, 1978) within the two major subassemblages of the *O*A is as follows:

Asprotilapia subassemblage			*Ophthalmotilapia* subassemblage		
Hap.[1]	*Troph.*	*Tilapia*	*Hap.*	*Troph.*	*Tilapia*
Callochromis	*Xenotilapia* (a few spp.)	—	—	*Cyathopharynx*	*Lestradea*
Xenotilapia (most spp.)	*Aulonocranus*	—	—		*Ophthalmotilapia*
*Grammatotria**	*Ectodus*	—	—		*Cunningtonia*

[1] *Hap.* = *Haplochromis* type; *Troph.* = *Tropheus* type; *Tilapia* = *Tilapia* type.

*In all specimens the apophysis is of the *Haplochromis* type on one side, and the *Tropheus* type on the other.

It is interesting that no true *Tilapia* type apophysis occurs amongst members of the *Asprotilapia* subassemblage, but that three of the four taxa in the *Ophthalmotilapia* subassemblage do have an apophysis of that type. In contrast, a *Haplochromis* type apophysis occurs in three members of the *Asprotilapia* subassemblage but not in any taxa of the *Ophthalmotilapia* subassemblage.

It must be borne in mind, however, that the *Tropheus* apophyseal type is structurally intermediate between the *Haplochromis* and *Tilapia* types (see Greenwood, 1978) and that in the *Asprotilapia* subassemblage certain taxa have more than one type of apophysis. Indeed, the three specimens of *Grammatotria lemairei* examined have a *Haplochromis* type apophysis on one side of the skull and a *Tropheus* type on the other.

It is also interesting to note that if the *Tropheus* category (of Greenwood, 1978), which Regan did not recognize, is ignored and the taxa in that category are returned to the one in which they were placed by Regan (1920), then the entire *Asprotilapia* subassemblage is of the *Haplochromis* type, and the *Ophthalmotilapia* subassemblage becomes exclusively of the *Tilapia* type.

Such a pattern might well be taken to argue against my earlier criticisms of the pharyngeal apophysis as an indicator of phyletic relationships at a high level of universality (Greenwood, 1978) and that, on the contrary, African cichlids can be divided into '*Tilapia*' and '*Haplochromis*' supralineages as suggested by Regan (1920).

If the latter argument is accepted, then the synapomorphies delimiting the *Ophthalmotilapia* assemblage as a whole must be considered as homoplasies developed independently in the two subassemblages recognised here. That assumption would produce a scheme of relationships less parsimonious than the one proposed above and earlier by Liem (1981). Also, the existence of intermediate conditions (i.e. the *Tropheus* type) in the structure of the apophysis, and of other cases where a classification based on apophyseal structure is incongruent with different and apparently synapomorphic characters (see Greenwood, 1978; Liem & Stewart, 1976) would seem to support the rejection of apophyseal structure as an indicator of phyletic relationships at the level proposed by Regan.

A review of other schemes of relationship suggested for members of the *Ophthalmotilapia* assemblage

Regan (1920 : 52) did not present detailed arguments for his views on the interrelationships of the Lake Tanganyika genera, which were strongly influenced by his assumption of there being a fundamental dichotomy of African cichlids into those with a '*Tilapia*' type apophysis, and those with a '*Haplochromis*' type (see above). As a result of this basic difference in approach, it is difficult to make direct comparisons between Regan's ideas and those put forward in this paper. However, some comments can be made on certain of Regan's suggested relationships involving *O*A members and taxa outside that assemblage.

For example, *Ophthalmotilapia* was grouped with *Cyathopharynx, Cunningtonia, Asprotilapia, Petrochromis* and the Malawian genus *Petrotilapia* (then considered a species of *Petrochromis*); furthermore, Regan suggested that *Ophthalmotilapia* was closely related to *Limnotilapia* (now synonymised with *Simochromis,* see Greenwood, 1979) and that it had '. . . given rise to *Cyathopharynx*'.

Petrochromis and *Petrotilapia* were included in this grouping because, in their dental morphology and pattern, they are strikingly similar to *Cunningtonia* (see p. 280 below).

No reasons were given for including *Asprotilapia,* a taxon quite unlike the others in its gross morphology and in its dentition; presumably the reason lay in Regan's (1920 : 42) belief that the 'Skeleton (is) essentially similar to that of *Ophthalmotilapia ventralis* . . .'. The skeletal features noted by Regan (1920 : 41 & 42) were, it should be emphasised, not those used in this paper; most can be treated as plesiomorph characters when used at the level of analysis involved here.

Presumably it was the same suite of skeletal characters which led Regan to suggest a close relationship between *Limnotilapia* (i.e. *Simochromis*) and *Ophthalmotilapia,* a relationship which I cannot accept since '*Limnotilapia*' apparently shares no derived features with any members of the *O*A.

Ectodus (as a putative ancestral morphotype) was grouped by Regan (1920 : 53) with *Callochromis, Xenotilapia* and *Grammatotria,* the taxa being given that order of increasing morphological derivation. Again no detailed reasons are given for this grouping, save that all its taxa have a '*Haplochromis*' type pharyngeal apophysis and small conical teeth. In effect, however, it approximates closely to the arrangement proposed in this paper.

Regan (1920 : 53) also included, albeit implicitly rather than explicitly, *Aulonocranus* and *Trematocara* with those genera listed in the previous paragraph. The association of *Aulonocranus* with *Trematocara* was, presumably, based on both genera having hypertrophied cephalic laterosensory canal systems (Regan, 1920 : 47); no other relationship with *Aulonocranus* was suggested, save that it is 'Intermediate between *Haplochromis* and *Trematocara.*' The linking of *Aulonocranus* and *Trematocara* with the *Ectodus*-*Grammatotria* group (see above) was apparently based on the common possession of small conical teeth and a '*Haplochromis*' type of pharyngeal apophysis.

That Regan did not consider there to be any relationship between his *Asprotilapia-Ophthalmotilapia* and his *Ectodus-Grammatotria* (+*Aulonocranus*) groups is doubtless due to his basic assumption that the endemic genera of Lake Tanganyika were derived from '. . .two ancestral types, one nearly related to *Limnotilapia* and the other to *Haplochromis*' (Regan, 1920 : 53).

After Regan's initial analysis of the Tanganyika cichlids, no further attempt to interrelate the endemic genera of the lake was made for more than fifty years. In 1972 Fryer & Iles paid considerable attention to this problem, in particular to the assumption that there was a basic diphyletic origin of the flock. However, despite their professed uncertainty about the value of the pharyngeal apophysis as an indicator of phyletic relationships, Fryer & Iles (1972 : 506, fig. 337) virtually followed Regan's (1920) scheme. They were, of course, able to include three genera described since that time, namely *Lestradea, Cardiopharynx* and *Ophthalmochromis. Cardiopharynx* is now considered a synonym of *Cyathopharynx* (see p. 282) and *Ophthalmochromis* was synonymised with *Ophthalmotilapia* by Liem (1981: 210–211).

As would be expected, Fryer & Iles considered *Ophthalmochromis* and *Cardiopharynx* to be the sister taxa of *Ophthalmotilapia* and *Cardiopharynx* respectively. Interestingly, they associated *Lestradea* with *Asprotilapia, Cunningtonia* and the *Ophthalmotilapia-Ophthalmochromis* pair, but gave no reasons for doing so. Their tentative alliance of *Cyathopharynx*+*Cardiopharynx* with *Lobochilotes* and *Limnotilapia* is not explained either, and only partly follows Regan who implied some relationship between *Limnotilapia* and *Lobochilotes,* but also included *Gephyrochromis, Simochromis* and *Tropheus* in the same group – again without a detailed explanation (Regan 1920 : 52). I can find no synapomorphic characters to support the idea of a close relationship between *Lobochilotes* and any member of the *Ophthalmotilapia* assemblage.

Like Regan, Fryer & Iles (1972 : fig. 337) treat *Aulonocranus* and *Trematocara* as close relatives, but give the two genera an origin separate from that of the taxa currently grouped in the *O*A.

Leptochromis (now renamed *Reganochromis,* see Whitley, 1928), a genus not mentioned in Regan's analysis, is included by Fryer & Iles as a member of their *Ectodus, Callochromis, Xenotilapia* lineage, but again no reasons are given. This suggested relationship is discussed on p. 278 below.

In effect, the main difference between the schemes proposed by Regan (1920) and Fryer & Iles (1972) lies in the latter authors not portraying any taxa in an ancestor-descendent relationship, as was implied, or stated explicitly, in Regan's treatment. Also, Fryer & Iles indicate a more distant relationship than did Regan between *Limnotilapia* (i.e. *Simochromis*) and other members of the latter author's *Ophthalmotilapia* group (see above, p. 275).

In their final analysis Fryer & Iles are less definite in their suggested relationships than was Regan (see figure 337 in Fryer & Iles, 1972 : 507); their phylogram was to be '. . . regarded as extremely tentative'.

Liem's (1981) wide ranging review of the *O*A is, in its treatment of anatomical and morphological detail, far more thorough than either of the other two reviews. It was also the first to employ a basically cladistic (*sensu* Hennig, 1966, phylogenetic *sensu* Wiley, 1981) methodology.

Liem brought together certain taxa from Regan's two major groups (see above p. 275), namely *Ectodus* with some elements of Regan's *Ophthalmotilapia-Asprotilapia* group, but excluded other taxa from his *Ectodus-Grammatotria* assemblage (see p. 275 above).

The present analysis (also cladistically based) finally brings together, in a single lineage, all but one pair of taxa from Regan's two groups, the exceptions being *Petrochromis* and the Malawian genus *Petrotilapia* (see above, p. 275). It also includes *Aulonocranus* (but not *Trematocara*) from a third group which Regan implied had some relationship with his *Callochromis-Grammatotria* lineage (Regan, 1920 : 53). Effectively it hypothesizes that the two major Regan groups are sister lineages within a larger taxon which, following Liem (1981), can be named, informally, the *Ophthalmotilapia* assemblage (see Fig. 14).

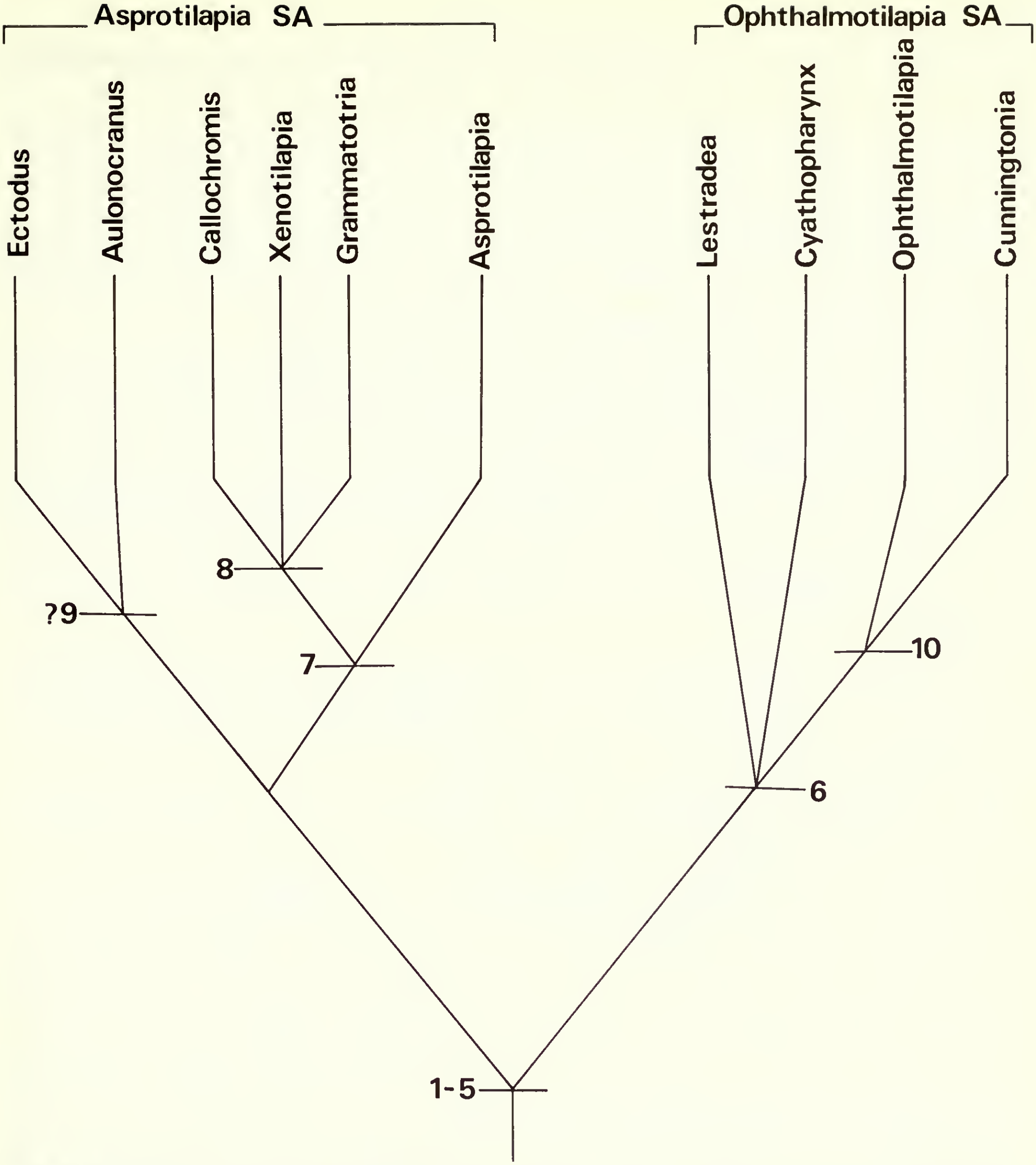
Asprotilapia SA
Ophthalmotilapia SA
Ectodus
Aulonocranus
Callochromis
Xenotilapia
Grammatotria
Asprotilapia
Lestradea
Cyathopharynx
Ophthalmotilapia
Cunningtonia
8
?9
7
10
6
1-5

Fig. 14 Cladogram for the *Ophthalmotilapia* assemblage based on the 10 apomorphic characters discussed in this paper. Page numbers, given in brackets after each numbered character, refer to those pages on which the character is discussed in detail.

An interrogation mark precedes character 9 since its apomorphic status is doubtful (see p. 272).

(1) Palatopterygoid gap (p. 254)
(2) Auricular process on the operculum (p. 259)
(3) Morphological features of the palatine bone (p. 257)
(4) Outline shape of the lachrymal (1st infraorbital bone), and the presence of six laterosensory canal pores (p. 259)
(5) Adductor fossa on the lateral aspect of the anguloarticular bone (p. 261)
(6) Intestine long and transversely coiled p. 264)
(7) Presence of a pharyngeal hanging pad and associated modifications to the gill-raker morphology (p. 265)
(8) Dentary with a distinct 'step' (p. 267)
(9) First branched pelvic fin ray produced (p. 272)
(10) Dorsal part of the flange behind the vertical part of the preopercular laterosensory canal not narrowing abruptly (p. 273)

Summary of the taxonomic conclusions and a discussion of the sister-group problem in these and other lake cichlids

The *Ophthalmotilapia* assemblage, originally comprising the genera *Ectodus, Lestradea, Asprotilapia, Cunningtonia* and *Ophthalmotilapia* (Liem, 1981) can now be expanded to include *Xenotilapia, Callochromis, Grammatotria, Aulonocranus* and *Cyathopharynx* (with which is synonymized *Cardiopharynx*).

Taxonomically, the assemblage is recognized as a monophyletic lineage on the grounds of its member species sharing a unique congruence of five apomorphic characters (pages 254–262; Fig. 14).

Two major sublineages can be recognized within the assemblage.

One, characterized by having a short and simple coiled intestine, comprises the genera *Ectodus, Aulonocranus, Asprotilapia, Xenochromis, Callochromis* and *Grammatotria.* It can be further subdivided on the basis of various synapomorphies shared by four of its members (see pages 263–274 and Fig. 14).

The other major sublineage contains *Lestradea, Ophthalmotilapia, Cunningtonia* and *Cyathopharynx,* species in which the intestine is long and complexly coiled (see pages 264–265). Attempts to subdivide this lineage have not proved satisfactory, but it would seem that *Lestradea* is the plesiomorph sister-group of the other three genera (pages 271–274 and Fig. 14); possibly amongst these three genera *Ophthalmotilapia* and *Cunningtonia* are sister taxa, but the entire group is, for the moment, probably best treated as an unresolved polychotomy.

No sister-group, or even a single taxon, has so far been satisfactorily identified amongst the cichlids of Lake Tanganyika. Regan's (1920 : 52) suggestion of close relationship between *Limnotilapia* (i.e. *Simochromis,* see Greenwood, 1979) and *Ophthalmotilapia* (and hence *Cyathopharynx, Asprotilapia* and *Cunningtonia* as well) cannot be corroborated on the basis of shared synapomorphies.

When comparisons are made with other Tanganyika taxa the results are equally unproductive except that two *O*A group synapomorphies occur, singly, in some species of '*Limnochromis*' and *Trematocara.*

For example, in *Trematocara marginata,* but in no other species, there is a poorly differentiated *O*A-like projection from the anteroventral angle of the lachrymal (see p. 259). A similar projection occurs in '*Limnochromis*' *permaxillaris* and '*L.*' *pfefferi,* both of which are now placed in Poll's genus *Gnathochromis.* Both the '*Limnochromis*' species and *Trematocara marginata* have only 5 pores in the lachrymal, but other '*Limnochromis*' species which lack the projection, '*L*' *otostigma, L. auritus* and *L. abeeli,* have 5 or 6 pores.

Neither *Trematocara* nor '*Limnochromis*' has the characteristically shaped lachrymal of the *O*A species, and the distribution pattern of the two *O*A group-features indicates an independent (i.e. homoplastic) origin in the two genera.

Regan's (1920 : 53) suggested relationship between *Aulonocranus* and *Trematocara* apparently stems from the hypertrophied laterosensory canals, and pores, present in both taxa. Apart from that feature, and the weak *O*A-type lachrymal peak in one species of *Trematocara,* there are no derived features uniquely shared by the two genera. Admittedly there is a trend amongst the *O*A species for there to be some degree of hypertrophy in the laterosensory canal system of the lachrymal. But, in the absence of other synapomorphies it would be unrealistic to use a trend character as a basis for suggesting group relationships, especially when that trend occurs in several other lineages as well. In this particular instance, too, the lowest degree of canal enlargement is found in those *O*A species with the least number of derived features (i.e. *Ectodus* and *Lestradea*), and which are therefore taken to be the plesiomorph members of their respective subassemblages.

The tentative phylogenetic schemes proposed by Fryer & Iles (1972 : 507, fig. 337) are not always arranged so as to suggest sister-group relationships with taxa outside the *O*A. They do, however, show *Leptochromis* (i.e. *Reganochromis*) as a sister taxon of *Ectodus, Callochromis, Xenotilapia* and *Grammatotria,* and *Aulonocranus* is paired with

Trematocara. Once again, there are no shared derived features to substantiate such relationships, and none which might indicate that either *Reganochromis* or *Trematocara* is the sister-group, or part of the sister-group, to the *Ophthalmotilapia* assemblage.

The only taxon which consistently shows more than a single *O*A group synapomorphy amongst a number of its species is the Malawian genus *Lethrinops.*

I have examined alizarin preparations and dry skeletons of five *Lethrinops* species, the type species *Lethrinops lethrinus*, and *L. praeorbitalis, L. parvidens, L. auritus* and *L. longimanus.* In all there is a distinct palatopterygoid gap and a well-defined, although not extensive *O*A type adductor fossa on the anguloarticular bone (Figs 15 & 16).

The palatopterygoid gap is relatively smaller than in most *O*A species, but in none of the *Lethrinops* species examined is there any contact between the palatine and the entopterygoid. Unlike members of the *O*A, the *Lethrinops* species have a much deeper entopterygoid, and one that either rests along the upper margin of the quadrate or slightly overlaps that bone medially. In *O*A species, most of the entopterygoid lies medial to the quadrate, and is thus largely obscured by it in lateral view. As a consequence of this spatial relationship the dorsal margin of the entopterygoid in *Lethrinops* lies at a level nearer the palatine head than it does in *O*A species.

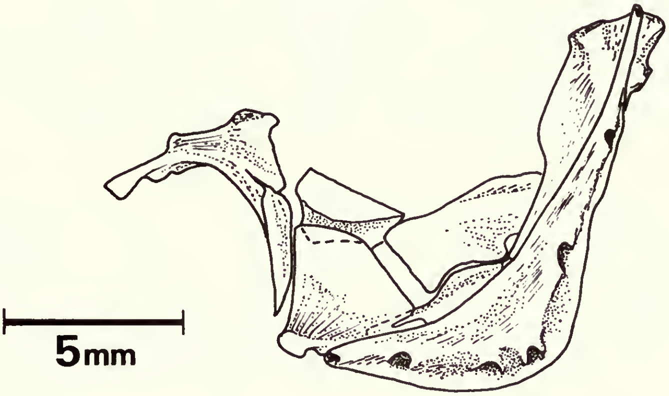

Fig. 15 Left suspensorium of *Lethrinops lethrinus.*

The shape of the palatine (Fig. 15) in *Lethrinops* differs somewhat from that in the *O*A taxa (see p. 257 above). Its posterior margin is slightly concave, and the angle between this margin and the head of the bone is less nearly rectangular; the posterodorsal margin contributing to the angle is also less acute in *Lethrinops;* indeed, in some specimens and species it is almost rounded. But, as in the *O*A species the body of the bone is expanded posteriorly so that the bone's proportions are nearer those of the *O*A type than that commonly found amongst African cichlids.

The occurrence of this particular palatine shape in association with a palatopterygoid gap raises the question of whether or not the two characters are correlated. That a similarly shaped palatine does occur in at least two species without a palatopterygoid gap (viz. *Limnochromis abeeli* [Lake Tanganyika] and *Astatotilapia macropsoides* [Lakes Edward and George]), would seem to argue against correlation, but the possibility requires further testing.

The adductor fossa in *Lethrinops* (Fig. 16) is well defined but, as compared with the fossa in members of the *Asprotilapia* subassemblage amongst the *O*A (p. 261) it is less extensive. It is, however, comparable with the fossa in members of the *Ophthalmotilapia* subassemblage (p. 265).

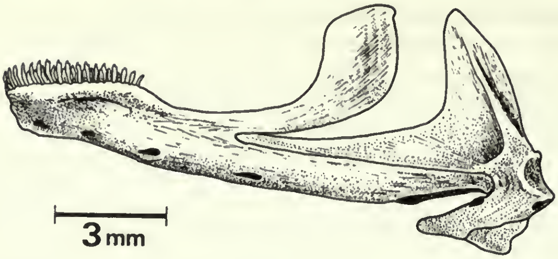

Fig. 16 Left dentary and anguloarticular of *Lethrinops lethrinus*, lateral view.

An adductor fossa of this type is not restricted to members of the *O*A, but also occurs in several seemingly unrelated taxa, including some '*Haplochromis*' species from Malawi (see p. 261). Thus, in itself, the fossa cannot be considered a unique apomorphy; its value as a group synapomorphy stems solely from its congruence with other apomorphic characters.

There is a third derived character found in the five *Lethrinops* species which is also present in one subgroup of the *O*A, namely a stepped dorsal margin to the dentary, with the teeth confined to the higher level of the step (Fig. 16). Amongst the *O*A taxa this feature is found only in *Xenotilapia, Callochromis* and *Grammatotria* (all members of the *Asprotilapia* subassemblage; see p. 267). Its restricted distribution within the *O*A considerably reduces its potential significance as a character indicative of a possible relationship between *Lethrinops* and the *O*A. That it apparently occurs only in these *O*A species and in *Lethrinops,* and that both groups have a palatopterygoid gap is, nevertheless, intriguing and requires further investigation.

Attempts to evaluate the two apomorphic features shared by *Lethrinops* and the *O*A in its entirety (i.e. the palatopterygoid gap and the adductor fossa) are hampered by lack of comparative data from the Malawi cichlids as a whole. A relatively superficial survey shows, however, that the adductor fossa is present only in some haplochromine species (see p. 261). Whether or not these haplochromines are closely related to *Lethrinops* has not been adequately tested, but preliminary investigations do not suggest that this is the case.

The situation regarding the palatopterygoid gap is different. I have examined specimens of all the described genera of Malawi fishes, but by no means all their included species. In none is there a palatopterygoid gap. Thus, the character appears restricted to *Lethrinops* and the *O*A (see also p. 255).

In summary, it seems that no group of Lake Tanganyika cichlids consistently shows one or more of the group synapomorphies for the *O*A. On the other hand, in Lake Malawi at least some species of *Lethrinops* share two derived features with all members of the *O*A, and only one of these features (the adductor fossa) occurs in other Malawi taxa. The *Lethrinops* species also have a third derived feature, the shape of the dentary, which is present in one lineage amongst the *O*A.

As it stands, this indication of a possible sister-group relationship between the *O*A and *Lethrinops* is no more than suggestive. It could well be refuted as an example of convergence when more is known about the interrelationships of the cichlids from Lake Malawi and those of Lake Tanganyika.

There are several cases of close similarity existing between certain features in endemic taxa of each lake, but few between species in those lakes and endemic taxa from Lake Victoria.

As examples one may mention that the dentition in *Cunningtonia* is virtually identical with that in *Petrotilapia* and there are marked similarities in the jaw anatomy of the two genera (*Petrochromis* from Lake Tanganyika can also be included in this example); or, the morphology of the dentary in *Asprotilapia* which is like that of *Labeotropheus* a Malawian genus also sharing several features with *Tropheus* from Lake Tanganyika. Finally, one can cite the many similarities in syncranial architecture existing between *Simochromis* of Tanganyika and the *Pseudotropheus* species complex of Lake Malawi.

These are by no means the only cases that can be, or have been, cited of supposed convergence or parallelism between the cichlid faunas of the two lakes (see Fryer & Iles, 1972). Adequate explanations for these similarities are, however, far more difficult to find.

An example of similarity involving much greater geographical separation than that between Tanganyika and Malawi, and one which incorporates a greater number of species as well as a mosaic distribution of similar characters amongst the species, involves two members of the *OA*, another, unrelated, genus from Lake Tanganyika, a Malawian taxon and *Neopharynx schwetzi*, a monotypic genus from the lower Fwa (Kasai drainage in southwestern Zaire; for a full description of *N. schwetzi*, see Poll, 1948).

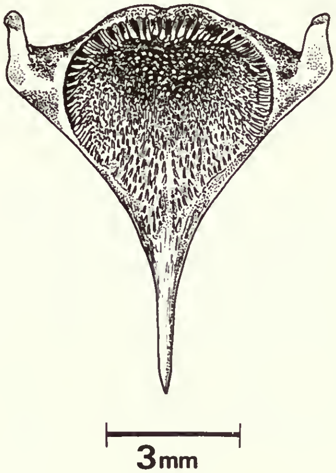

Fig. 17 Lower pharyngeal bone of *Neopharynx schwetzi*, occlusal view (from a specimen in paratypical series, MRAC 71291–71299).

Neopharynx schwetzi has a lower pharyngeal bone morphologically and dentally almost identical with that of *Cyathopharynx* (see Figs 17 & 24). Its oral dentition, in contrast, is virtually identical with that in *Petrochromis* (Tanganyika) and *Petrotilapia* (Malawi), and is quite unlike that in *Cyathopharynx*. As far as the morphology of the teeth is concerned, but not their distribution on the dentary, *Neopharynx* also closely resembles *Cunningtonia* of Lake Tanganyika. It differs from all three taxa in the shape of its premaxilla, but the morphology of the premaxillary teeth is, as might be expected, very similar in all four genera.

The relationships of *Neopharynx* have yet to be established; probably they lie with two other Fwa endemics, *Cyclopharynx* and *Callopharynx*, genera having an extreme development of the *Neopharynx-Cyathopharynx* type of lower pharyngeal bone (for details see Poll, 1948).

Neopharynx has neither an *O*A type lachrymal, a palatopterygoid gap, nor an *O*A-type of adductor fossa, and the shape of its palatine bone is close to the generalized form. Thus the similarities between *Neopharynx*, *Cyathopharynx* and *Cunningtonia* are undoubtedly homoplastic, as most probably are the similarities shared with *Petrochromis* and *Petrotilapia*.

The *Neopharynx* example underlines the problems involved in attempting to work out interrelationships amongst cichlid fishes, as do the repeated appearances of certain derived features shown by members of the *Ophthalmotilapia* assemblage in species which appear to be but distantly related to the *O*A.

Surmises about the interrelationships of African lake cichlids have, I believe, been unduly influenced, perhaps even inhibited, by three major factors. Firstly, the idea that there are two basic lineages, a '*Tilapia*' line and a '*Haplochromis*' one (see discussion in Greenwood, 1978; also p. 274 above). Secondly, that the major lakes are, faunistically, closed basins and have been so almost since their inception, with the result that the cichlids of a lake are presumed to have evolved from one or a few ancestral species originally trapped there (see discussion in Fryer & Iles, 1972; and Greenwood, 1974). In other words, assumed histories for the lakes have been given too great a weight in deciding whether a feature was the result of convergence, parallelism, or the consequence of common ancestry.

The third, and overriding, factor is a paucity of specific and critical studies on the phylogeny of the fishes. Overall resemblances, or the use of characters without adequate outgroup comparisons, are often major weaknesses influencing decisions on relationships.

The effect of these three factors has resulted in a tendency to restrict the search for sister-groups to a single lake and to the appropriate '*Tilapia*' or '*Haplochromis*' lineage. Admittedly, at lower levels of universality sister species are generally to be found within the same lake or proto-lake system (Greenwood, 1980); the problems arise when attempting to establish relationships at somewhat higher taxonomic levels. The *Ophthalmotilapia* assemblage, and the search for its sister-group are good examples of problems encountered at these two levels.

The existence of endemic species flocks, the superficially close similarity of species in different flocks, and indeed of many different taxa outside the lakes, all help to complicate the issue. Under such circumstances the possibility and probability of homoplasy are theoretically enhanced, as in practice are the problems associated with their resolution.

What is needed to resolve these problems are tests of the assumption that a so-called species flock is really of monophyletic origin. If a lake's cichlid fauna was derived from a few species which are not true sister species, and if the true sister taxa were the ancestors of another flock, then the situation suggested by the apparent relationship of *Lethrinops* (Malawi) and the *O*A (Tanganyika) could well be a real one. The idea first put forward by Regan (1922) that the Malawi 'flock' carries indicators of its monophyly must be seriously questioned (Greenwood, in press). No indicators of monophyly have been suggested for the Tanganyika 'flock' (even at the levels of the supposed '*Tilapia*' and '*Haplochromis*' type basic stocks). The possibility of a close relationship between the faunas of the two lakes deserves very careful examination.

The status of *Cyathopharynx* Regan, 1920 and *Cardiopharynx* Poll, 1942

In his original description of the monotypic genus *Cardiopharynx,* Poll (1942 : 346) noted the great similarity between its peculiarly shaped lower pharyngeal bone and the lower pharyngeal of *Cyathopharynx.* He differentiated the two genera because *Cardiopharynx* has, as compared with *Cyathopharynx*:

(i) Larger scales (36–38 *cf* 48–64 in a longitudinal series (see Poll, 1956 : 127).
(ii) Jaw teeth in two rows, the teeth, in both jaws, of equal size (*cf* 3–5 rows; teeth in the outer row larger than those of the inner rows).
(iii) Dentigerous surface of the lower pharyngeal bone cardiform (*cf* rounded in *Cyathopharynx*)
(iv) Supraoccipital extending forward to a level above the anterior margin of the orbit (*cf* to the mid-orbital region only)
(v) Parietal crests ending above the centre of the orbit (*cf* extending to a point above the posterior part of the orbit)
(vi) More vertebrae (36, i.e. 17 + 19) *cf* 32–34 (i.e. 16 or 17 + 16 or 17)

Poll gives no reasons why these characters should be used to separate the taxa at a generic level, and neither does he indicate why the great similarity in pharyngeal morphology, and its uniqueness, should be outweighed as an indicator of close phyletic relationship by the diagnostic characters he enumerates.

None of these latter features can be considered uniquely apomorphic for *Cardiopharynx*, and now that more material is available several are found to be less trenchant than was first thought to be the case, as the following comments show.

The teeth in both jaws of all *Cardiopharynx* specimens I examined are invariably arranged in two rows, but in *Cyathopharynx* there is a greater variation than was intimated by Poll (1942 & 1956). In the majority of specimens examined, the inner premaxillary row is, in places, irregularly arranged so as to give the appearance of a double row wherever the irregularities occur. Occasionally there are specimens in which the inner tooth row is clearly and regularly double, thus giving a total count of three tooth rows; also occasionally it is distinctly single, giving a total of two rows. In none of the specimens is there a total of more than three premaxillary rows. The inner row of teeth in the dentary is generally single; in a few fishes, however, it is somewhat irregular and so comes to resemble the modal condition in the premaxilla.

Contrary to Poll (1946), I can find no marked difference between the taxa in the relative size of inner and outer teeth. In both genera the outer teeth, in both jaws, are clearly taller and stouter than those of the inner row or rows, and not of equal size in *Cardiopharynx* as claimed by Poll. The most that can be said is that in *Cardiopharynx* the size difference between outer and inner row teeth is a little less marked than in *Cyathopharynx.*

In a later redescription of both taxa, Poll (1956) commented on the outer teeth of *Cardiopharynx* being more or less tricuspid in young fishes, but he gave no size-range over which tricuspid teeth are found. In specimens 60–105 mm SL I have examined, there are no outer tricuspids, whereas in specimens of *Cyathopharynx* of a comparable size range and up to 112 mm SL, distinctly, and also weakly, tricuspid teeth do occur. In larger *Cyathopharynx* specimens the teeth are exclusively and clearly unicuspid.

The difference in the shape of the dentigerous surface of the lower pharyngeal bone (iii above, p. 282) is due entirely to a marked median depression in the posterior face of the bone and of the toothed area in *Cardiopharynx.* In *Cyathopharynx* this margin of the bone is slightly and more broadly indented, and there is no indentation of the posterior tooth row (Fig. 23).

In all other respects the lower pharyngeal bone in both taxa is identical. As noted above (p. 271) it represents a uniquely derived condition amongst the cichlids of Lake Tanganyika.

The shape of the pharyngeal teeth, tall and slender, with spatulate crowns that are not broader than the neck, and their cardiform pattern on the alveolar surface of the bone, is the same in both genera (Fig. 24). Likewise, the morphology of the principal upper pharyngeal bones is identical, as is the morphology and pattern of their teeth. Unlike the lower teeth, those on the upper pharyngeal bones do have a slight, shoulder-like cusp at the base of the spatulate crown surface.

The anterior point reached by the supraoccipital and parietal crests (iv & v above) is variable intragenerically. In the skulls I have examined there are specimens from each genus showing conditions intermediate between those originally used as diagnostic features for the two genera.

Finally, there are the supposedly intergeneric differences in vertebral number (vi above). I have examined 15 specimens of *Cardiopharynx schoutedeni* (13 from radiographs, 2 as alizarin preparations), and 12 of *Cyathopharynx furcifer* (10 from radiographs and 2 dry skeletons), and obtained the following counts:

Cardiopharynx: Total number (excluding the fused U_1–PU_1 centra) 33 (f5) and 34 (f10), comprising 15 (f1), 16 (f7) or 17 (f7) abdominal and 16 (f1), 17 (f9) or 18 (f5) caudal elements.

Cyathopharynx: Total number (excluding the fused U_1–PU_1 centra) 32 (f5) 33 (f6) or 34 (f1), comprising 16 (f9) or 17 (f3) abdominal and 16 (f7) or 17 (f5) caudal elements.

The differences in range are not very marked and there is a complete overlap in other counts, but with a slight difference in the modal number for total [34 *cf* 33] and abdominal counts [17 *cf* 16] for *Cardiopharynx* and *Cyathopharynx* respectively.

Thus, of Poll's (1942) original diagnostic features, only the difference in scale size remains.

There are, however, other differences which were noted in the original diagnosis. *Cyathopharynx* has proportionately longer pelvic fins, in males the tip of this fin reaches the last anal fin ray or even to as far as the caudal fin fork; in *Cardiopharynx* it reaches only to about the middle of the anal fin. Also, in *Cyathopharynx* the first pelvic ray is clearly the longest whereas in *Cardiopharynx* either the first and second rays are equally protracted or the second ray may be the longest.

Other differences involve neurocranial shape (Figs 18 & 19). *Cardiopharynx* has a shallower skull than does *Cyathopharynx,* the prootic portion of its otic bulla is more inflated, and the interorbital region is much narrower.

Undoubtedly the two taxa are distinguishable. The problem is to decide at what taxonomic level their separation should be recognized.

To recognize two genera on the basis of the differences discussed above is to obscure the fact that, amongst the Lake Tanganyika cichlids, *Cyathopharynx* and *Cardiopharynx* share a unique apomorphy (the form of the lower pharyngeal bone) which would indicate a common ancestry not shared with any other taxon. That relationship is, I believe, best indicated by treating the two species as members of a single genus, *Cyathopharynx* Regan, 1920.

Cyathopharynx Regan, 1920

Cyathopharynx Regan, 1920. *Ann. Mag. nat. Hist.* (9), **5:** 42–43.
Cardiopharynx Poll, 1942. *Revue Zool. Bot. afr.,* **36:** 346–347.

TYPE SPECIES. *Tilapia grandoculis* Boulenger, 1899. *Trans. zool. Soc. Lond.* **15:** 94, pl. XIX, fig. 6.

Poll (1946 : 283–4) has synonymized this species with *C. furcifer* (Blgr), 1898.

DIAGNOSIS. A member of the *Ophthalmotilapia* assemblage, distinguished from other members of that group by having a cardiform dentigerous surface to the lower pharyngeal bone, the body of which is inflated and nearly cardiform in outline.

Cyathopharynx is distinguished from other species with a cardiform alveolar surface to the lower pharyngeal bone by, among other features, its *O*A group characters (see p. 262) and by the marked elongation of the first, or first and second pelvic fin rays in adult male fishes; these protracted rays extend to at least the middle of the anal fin, and in one species, sometimes as far as the fork of the caudal fin.

Description

Neurocranium (Figs 18 & 19). In its general outline, the skull differs little from that of the generalized haplochromine type in which the preorbital profile is slightly decurved. The orbit, however, is relatively larger than in a generalized skull, and the otico-occipital region is shorter, a correlate, probably, of the enlarged orbit since the ethmoid region retains the same proportions as in a generalized skull.

The ventral apophysis for the upper pharyngeal bones is of a weak '*Tropheus*' type, in which the basioccipital barely contributes to the articular surface (see Greenwood, 1978; also p. 274 above).

Suspensorium (Figs 1C & D). As in other members of the *Ophthalmotilapia* assemblage, there is a distinct palatopterygoid gap (see p. 255), and the entopterygoid is shallow, with only one-third to one-quarter of its depth visible above the quadrate margin. The hyomadibula has a narrow flange anterior and dorsal to the symplectic process. The shape and proportions of the symplectic are typically those of an *O*A species (see p. 256).

Infraorbital series (Figs 3A & F). The lachrymal bone (1st infraorbital) has the typical outline shape, and the anteroventral process, of an *O*A taxon (see p. 259). There are six pores opening from the laterosensory canal system, the tubular part of which is somewhat

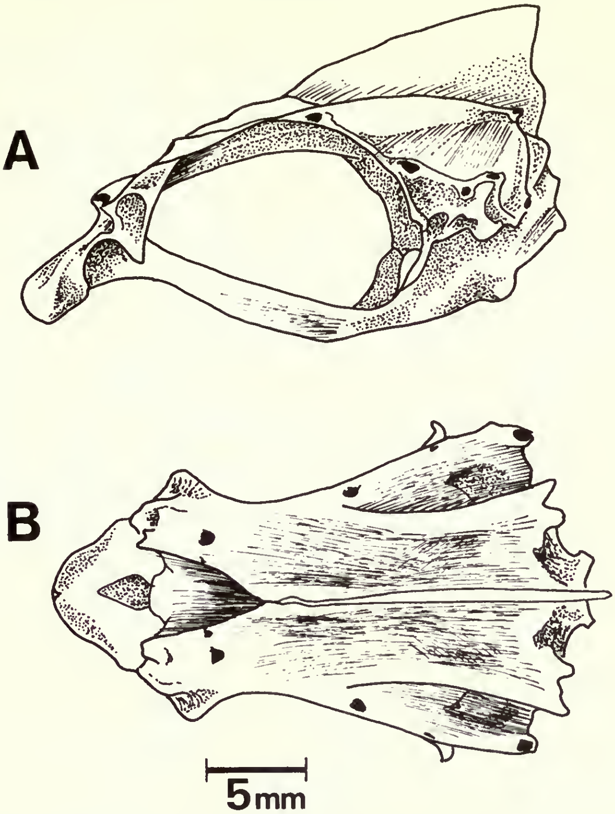

Fig. 18 Neurocranium of *Cyathopharynx furcifer* in : A, left lateral view; B, dorsal view.

inflated. The pores, however, do not show a corresponding enlargement (i.e. they do not deviate noticeably from the generalized condition). The other infraorbital bones are little more than tubular ossifications around the sensory canal, but do have low dorsal and ventral keels.

Myology. Division I of the *adductor mandibulae* complex has an extensive origin along the vertical limb of the preoperculum, but division II has its preopercular origin mainly from the horizontal limb of that bone; only a small area extends onto the vertical limb.

The dorsal gill-arch muscles compare closely, in most respects, with those of other *O*A species (see Liem, 1981 : 196–7 & 205, & fig. 8; also p. 258 above). The *retractor dorsalis* muscles are especially well developed with, in some individuals of both species, indications of a subdivison into dorsal and ventral components.

Dentition (Fig. 20). Some aspects of the oral dentition have been commented upon already (p. 283 above). The outer row teeth in both jaws are tall and slender. In *C. furcifer* the crown is slightly broader than the neck and shaft of the tooth, whereas in *C. schoutedeni* the crown is no wider than the shaft. The crowns are slightly recurved in both species.

Premaxillary outer row teeth are aligned vertically to the alveolar surface, but in the dentary the teeth situated anteriorly and anterolaterally are procumbent. The posterior dentary teeth are vertical, those of *C. furcifer* continuing for some distance up the coronoid process.

Inner row teeth in both jaws, and both species, are noticeably smaller than those of the outer row, and are implanted so as to lie almost horizontally.

Mouth. The lips are thin, and the gape is horizontal.

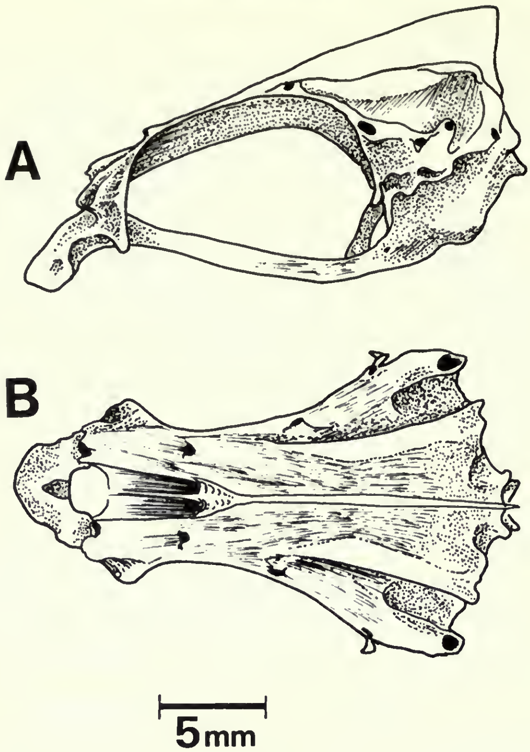

Fig. 19 Neurocranium of *Cyathopharynx schoutedeni* in : A, left lateral view; B, dorsal view.

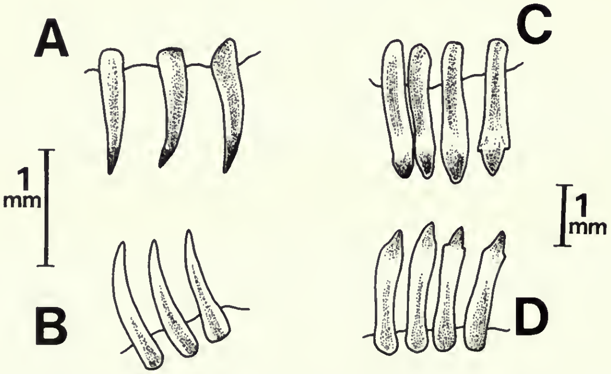

Fig. 20 Outer row jaw teeth (drawn *in situ*) from : A & B, *Cyathopharynx schoutedeni*, specimen 103 mm SL (premaxillae and dentary respectively); C & D, *C. furcifer*, specimen 113 mm SL (premaxilla and dentary, respectively). Dentary teeth viewed from below.

Jaws. The dentary in both species is a moderately slender bone, shallower and less robust in *C. schoutedeni* than in *C. furcifer* (Fig. 21). Anteriorly and anterolaterally the dorsal aspect of the bone is expanded into a broad surface which extends outwards to overhang, as a narrow shelf, the body of the bone. The tooth rows occupy only the outermost part of the surface, with the result that there is a wide expanse of bone lying medial to them. The laterosensory canal system and its openings in *C. furcifer* are more cavernous than those in *C. schoutedeni.*

The anguloarticular has a well-defined but short fossa for the *adductor mandibulae* muscle, with the ridge delimiting its anterior margin particularly deep and prominent.

The premaxilla (Fig. 22) has no especially outstanding features.

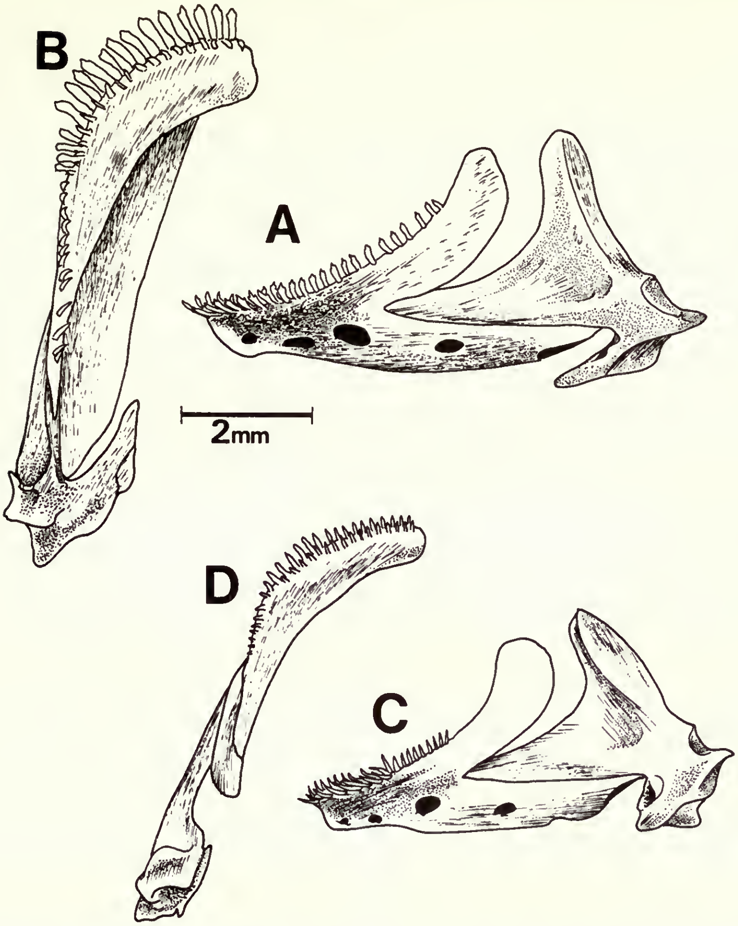

Fig. 21 Dentary and anguloarticular, in left lateral and occlusal views respectively, of: A & B, *Cyathopharynx furcifer*; C & D, *C. schoutedeni*.

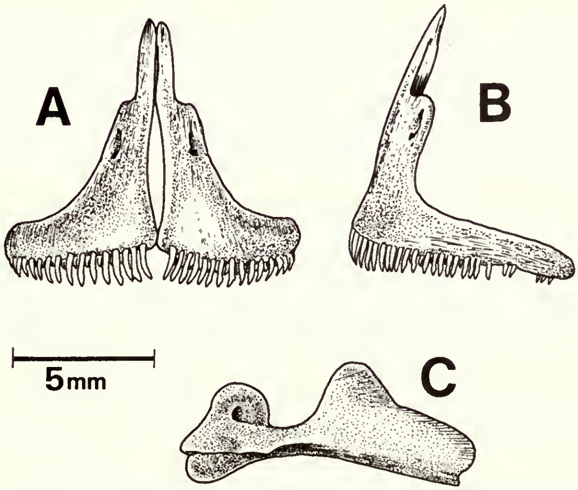

Fig. 22 A & B, premaxilla of *Cyathopharynx furcifer*, anterior and lateral view; C, maxilla (left) seen from a slightly ventrolateral viewpoint.

As compared with the generalized type of maxilla, that in *Cyathopharynx* is foreshortened and has a well-developed, long-based posterior process (see also p. 269).

The pharyngeal bones. The shape and other peculiar features of the lower pharyngeal bone (Fig. 23) are described on page 283.

The upper pharyngeal bones differ less markedly from the usual condition seen in African cichlids. The outline of the alveolar surface of the major element (pharyngobranchial 3) is noticeably ovoid, but otherwise differs little from the generalised condition. Their principal difference lies in the relatively greater alveolar surface area, and its more elongate proportions. Other differences are found in the less prominent facets for articulation with the 3rd and 4th epibranchials, and in the lower summit facet (nomenclature following Barel *et al.,* 1976 : 214, fig. 26).

The lower pharyngeal teeth (Fig. 24) are slender, near cylindrical in cross-section and are closely packed. Those at the periphery of the dentigerous area are weakly curved, the others

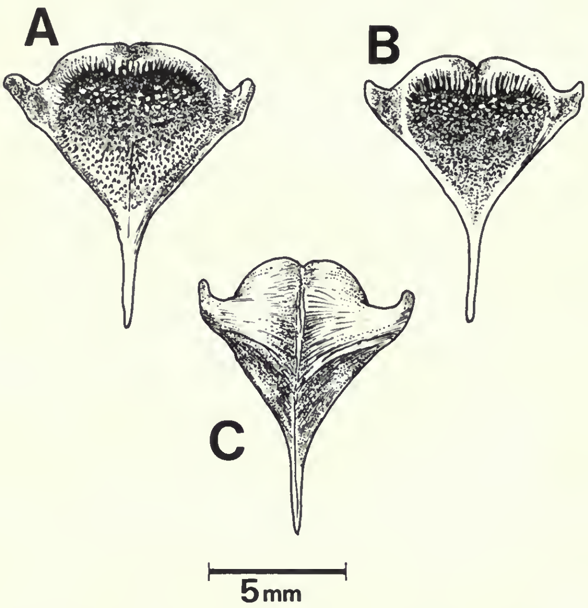

Fig. 23 Lower pharyngeal bone, in occlusal view of: A, *Cyathopharynx furcifer;* B, *C. schoutedeni,* and, in ventral view, C, of *C. furcifer.*

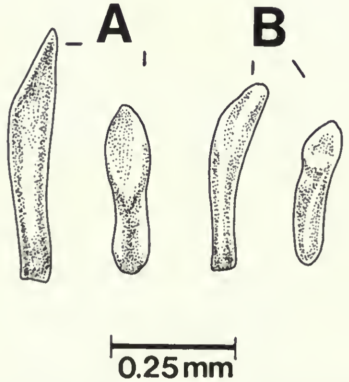

Fig. 24 *Cyathopharynx furcifer,* pharyngeal teeth (lateral and semiocclusal views) from : A, the posterior; and B, anterior dental fields.

erect. There is a noticeable and rapid increase in the height of the teeth forming the posterior 5 or 6 rows, with the teeth of the posterior row tallest and stoutest. The elongate crown of each tooth is flat, and slopes gently upwards and backwards. There is no indication of a low shoulder-like projection or cusp at the base of the crown.

The shape and dense arrangement of the upper pharyngeal teeth are very similar to those of the lower bone, the teeth differing only in having a small shoulder or cusp at the base of the posteriorly directed crown.

Vertebrae. Regan (1920 : 43), in his original description of *Cyathopharynx,* noted that the third vertebra lacks an inferior apophysis, from which the *retractor dorsalis* muscles originate. In four of the five dry skeletons and alizarin preparations I examined, a low apophysis is present on the fourth centrum in one fish and on the fifth centrum in three others, but none is present in the fifth specimen.

Vertebral counts for the two species are given on page 283.

Squamation. Scales on the body are weakly ctenoid except for the cycloid scales on the chest and belly. Those covering the thoracic region are small, and are fairly abruptly demarcated from the larger scales on the ventral flanks and the belly.

The two *Cyathopharynx* species differ, disjunctly, in the size of their body scales, with *C. schoutedeni* having 36–38 scales in a longitudinal series, and *C. furcifer* 48–64. The species also differ, slightly, in the posterior extension of the upper lateral line pore scales, those in *C. furcifer* usually extending almost to the caudal fin base, whereas in *C. schoutedeni* the pore scales terminate at a level 3 or 4 scale rows anterior to the caudal base. There is, however, some interspecific overlap in this feature.

Fins. Little can be added to the description (p. 272) of the protracted first or first and second pelvic fin rays in adult males. In females and juvenile males these rays are also noticeably longer than the others, but usually do not extend beyond the level of the anus; exceptionally they may reach the spinous part of that fin.

The caudal fin is forked; adult males have the two upper- and lowermost principal branched rays produced into fine filaments. Rows of small, barely overlapping scales are present on the fin membrane (except between the three middle rays), and extend to the level of the fork.

Gut. The intestine is long (*ca* 3 to 4 times SL) and complexly coiled in a predominantly transverse direction (see p. 264).

Contained species

Cyathopharynx furcifer (Blgr) 1898
Cyathopharynx schoutedeni (Poll) 1942

Both are lacustrine species endemic to Lake Tanganyika; for detailed descriptions, figures and biological data see Poll (1956 : 130–137 & 125–130 for the species respectively).

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Osteology, genitalia and the relationships of *Acanthodactylus* (Reptilia: Lacertidae)

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Synopsis

Acanthodactylus is reassessed, supplementing the external features previously used with new data from the skeleton and hemipenis. The genus appears to be closely related to *Eremias* and *Mesalina* rather than to *Latastia* as was previously thought, and *'Eremias' guineensis* is confirmed as an *Acanthodactylus.*

It is suggested that genitalia have an enhanced propensity to 'store' evidence of shared evolutionary experience in the form of common characters among descendants, when compared with other organ systems. Such characters deserve relatively high weight in assessing relationships. However, not all genital characters can be interpreted in this way for some seem likely to have evolved as physical isolating mechanisms between similar species and, in such cases, closely related forms may have radically different genitalia. Differences of this kind, together with some osteological features, have proved important in establishing the species status of several forms usually regarded as subspecies or varieties. Thus the four subspecies of *A. cantoris* are now accorded full species status as *A. cantoris, A. blanfordii, A. schmidti* and *A. arabicus* and a similar upgrading may well be appropriate for two taxa usually subsumed in *A. tristrami: A.* (*t.*) *tristrami* and *A.* (*t.*) *orientalis.* Within the *A. pardalis* complex, *A. pardalis, A. maculatus* and *A. spinicauda* are regarded as separate species and the form listed by

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Boulenger (1921) as var. *bedriagai* is treated as a subspecies of *A. pardalis;* a similar un-named West Moroccan population is also assigned to this species. Recently available material makes it probable that *A. grandis* and *A. fraseri* are closely related and perhaps allocatable to the same highly variable species. Within the *A. scutellatus* group the following taxa recognized by Bons and Girot (1962) are assigned to *A. scutellatus* itself: *A. s. scutellatus, A. s. audouini, A. s. hardyi, A. i. inornatus* and *A. dumerilii. A. longipes* is retained as a separate species and the same status is given to *A. aureus* which Bons and Girot regarded as a subspecies of *A. inornatus.* Geographical variation requires considerable further study in a number of taxa including the *A. grandis* complex, *A. boskianus* and the *A. scutellatus* group but a number of currently recognized subspecies are invalid such as *A. tristrami iracensis* Schmidt, 1939 (=*A.* (*t.*) *orientalis*), *A. pardalis latastii* (=*A. maculatus*) and probably several of the forms in the *A. scutellatus* group.

An attempt has been made to estimate a phylogeny for the species of *Acanthodactylus,* although considerable character conflict exists.

Introduction

The lacertid lizard genus *Acanthodactylus* Wiegmann, 1834 contains about 26 species. It occurs from Spain and Portugal across the Sahara desert and its periphery to the Red Sea, over most of Arabia and as far north as Cyprus and the Syrian–Turkish border; it also extends through Iraq, south and east Iran, south Afghanistan, Pakistan and northwest India. All its members are quite small, maximum body sizes of populations varying from about 52 mm to around 105 mm from snout to vent. They are diurnal and essentially ground-dwelling lizards usually found in relatively flat, often sandy situations and occurring in a wide variety of dry habitats which usually have at least some vegetation and range from open woodland to the borders of quite severe desert. Substrates occupied vary from quite hard loess and clay to aeolian sand. All species appear to be mainly active hunters and feed largely on small invertebrates including ants. Body temperatures of normally active animals are usually in the range 36° to 41° C (personal observations; Duvdevani & Borut, 1974*a*). Like most open-country lizards, *Acanthodactylus* species are probably very prone to bird predation and are also taken by other vertebrates such as snakes and monitor lizards (*Varanus*). Predator avoidance seems to depend largely on crypsis (colour match with substrate is often very good), fleeing, tail autotomy and the use of burrows. All species are oviparous and usual clutch size varies from two to about seven eggs, females in many populations appearing to produce more than one clutch annually. The majority of forms seem to mature within a year of hatching although some, like *A. erythrurus* in Spain and Portugal, may take two seasons.

The most detailed synopsis of the genus to date is that of Boulenger (1921) which although inevitably to some extent out dated, remains extremely useful, providing detailed descriptions of many forms. However, the amount of material available for study has increased massively over the past fifty years. In particular, specimens from many areas previously unsampled, such as much of the Sahara desert and Arabia, have been obtained. Furthermore, both Boulenger and subsequent workers have depended almost entirely on external characters. As there are reasons for believing that these on their own can be misleading when judging lacertid relationships (see for example Arnold, 1973) it seems worthwhile to increase the range of characters considered and, in the present paper, osteology and the structure of the hemipenis are taken into account.

What follows is not a formal revision but an overview of *Acanthodactylus* is given paying especial attention to the objective reality of the genus, species boundaries and, so far as they can be judged, inter-relationships of its members. Although the results presented here differ considerably from previously held opinions, the genus still requires a more detailed appraisal based on the large but scattered collections available in continental Europe and North America.

In this paper, the methods of phylogeny estimation employed are those discussed by Arnold (1981*a*). They depend largely but not entirely on Hennig's (1950, 1966) precept that joint possession of a derived character state is *prima facie* evidence of relationship. The word relationship is used in its genealogical sense: two species are more closely related to each other than to a third if they share a common ancestor not shared by that form. The following terms coined by Hennig are used, together with the adjectives derived from them: *apomorphy*—a derived character state; *synapomorphy*—a derived character state shared by two or more species and possibly indicating their relationship to each other; *plesiomorphy*—a primitive character state; *symplesiomorphy*—a primitive character state shared by two or more species, it does not indicate their relationship. *Monophyletic* and *holophyletic* are used in the sense of Ashlock (1974).

Abbreviations used

BM(NH)—British Museum (Natural History), London; CAS—California Academy of Sciences, San Francisco; CM—Carnegie Museum, Pittsburgh; EBD—Estación Biológica de Doñana, Seville); INHM—Iraq Natural History Museum, Baghdad; JUM—Jordan University Museum; MCZ—Museum of Comparative Zoology, Harvard; NMW—Naturhistorisches Museum, Vienna; RSM—Royal Scottish Museum; USNM—United States National Museum, Washington.

The reality of the genus *Acanthodactylus*

On the basis of external features, Boulenger (1918*a*) described the genus *Acanthodactylus* as 'un des plus naturels et des plus nettement délimités de la famille des Lacertides'. Examination of skeletal and hemipenial characters provides additional support for Boulenger's view and *Acanthodactylus* is confirmed as a clearly defined assemblage that shows no integration into other genera. Most of its features are found in the lizard usually known as *Eremias guineensis* but it is certain that this form should really be included in *Acanthodactylus* (see p. 296). Features present in all or most species are listed below.

1. Frontal bones completely fused in adults and at least largely so in juveniles.
2. Often a fontanelle in the anterior wall of the orbit between the frontal and prefrontal bones.
3. A backwardly directed spur of jugal bone absent.
4. Parietal fontanelle present,
5. Parietal bone not projecting backwards over the supraoccipital.
6. Postorbital and postfrontal bones usually separate (fused only in *A. cantoris*).
7. Postorbital bone not filling supratemporal foramen.
8. Parietal and squamosal bones not usually in contact.
9. Pterygoid teeth present or absent (often considerable intraspecific variation).
10. Epipterygoid not usually in direct contact with pro-otic bone.
11. Fourteen scleral ossicles present in each eye.
12. Scleral ossicle number 14 (following numbering system of Gugg, 1939) lacks a radially directed peripheral section (see Fig. 1).
13. Number of presacral vertebrae ranges from 23 to 27, in most cases 23–26.
14. In the post-thoracic series of free dorsal ribs, the longer anterior ribs are fewer than the shorter posterior ones.
15. Ribs on last presacral vertebra very reduced or absent.

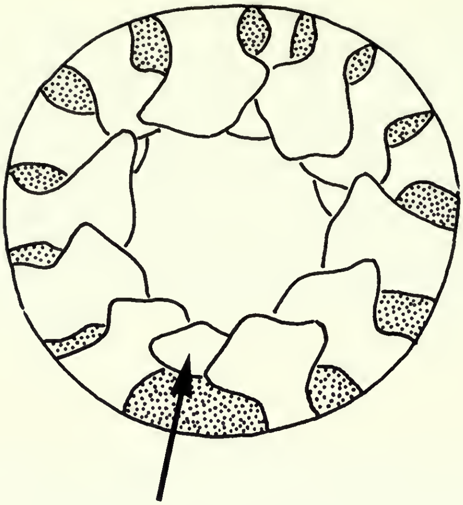

Fig. 1 Scleral ossicles of *Acanthodactylus*; arrow indicates scleral ossicle 14 which lacks a radially directed peripheral section.

16. Sternum with a more or less heart-shaped fontanelle, which is sometimes divided into left and right sections.
17. Sternal: xiphisternal rib formula 3 : 2 or less commonly 3 : 1.
18. Clavicle expanded medially with a large fenestra in this region, so that the bone forms an uninterrupted loop.
19. Interclavicle cruciform, the lateral arms usually directed obliquely forwards.
20. Only the principal coracoid foramen present.
21. Caudal vertebrae of the C-type (Arnold, 1973: 305); that is, the most anterior autotomic vertebrae have two pairs of transverse processes, the members of the posterior one being longer and directed obliquely backwards.
22. Hemipenis and armature usually asymmetrical with medial side reduced (see p. 300).
23. Hemipenis with an armature consisting of a flat intramuscular plate, one or two clavulae and short connectors.
24. In species where the hemipenis and armature is not very reduced there may be more than four connectors.
25. Nostril closable by a valve hinging on the posterior side of the opening.
26. Nostril nearly always situated between a postnasal, an internasal and the first upper labial (not in *A. guineensis,* although the situation in this species is derivable from that found in other *Acanthodactylus,* see Fig. 2).
27. First upper labial broad above but sides converge downwards (not in *A. guineensis*; see comments about previous character).
28. Occipital scale reduced or, more usually absent.
29. A distinct collar of imbricate scales beneath neck.
30. Dorsals small and granular or larger, imbricate and keeled with rounded posterior borders.
31. Maximum number of ventral scales in a row across the belly varies from 8 to 18.
32. Toes with three longitudinal rows of scales around them and fingers with three or four rows.
33. Subdigital lamellae keeled.
34. Lateral rows of scales on the toes and sometimes fingers forming pectinations.
35. Femoral pores present.
36. Tail more or less cylindrical, longer than body.

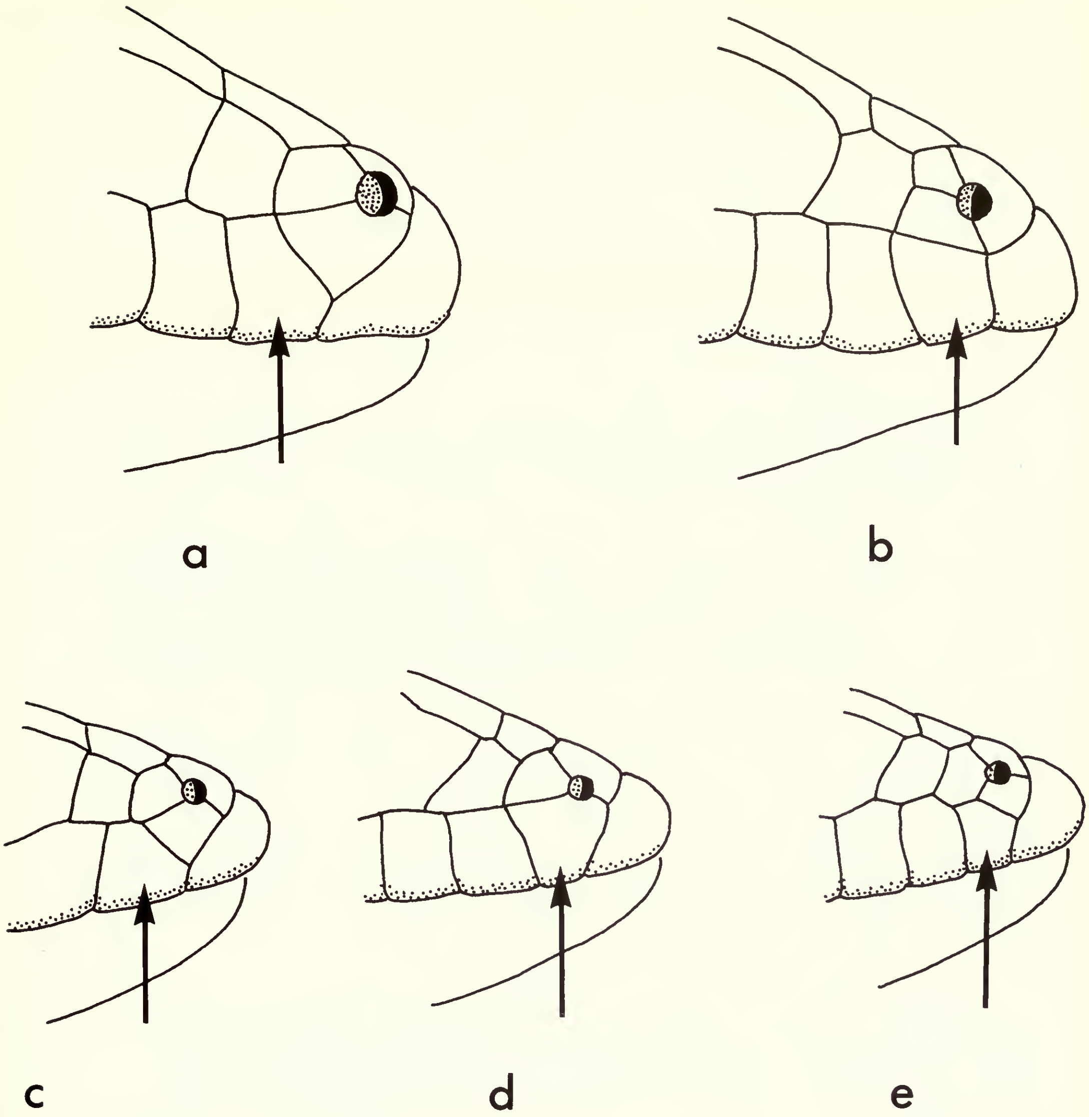

Fig. 2 Right nasal regions of *Eremias* and *Acanthodactylus*: (a) *'Eremias'* (=*Acanthodactylus*) *guineensis*, adult: (b) *Eremias nitida*, adult: (c) '*Eremias*' (=*Acanthodactylus*) *guineensis*, juvenile: (d) *Acanthodactylus erythrurus lineomaculatus*, juvenile: (e) *A. e. lineomaculatus*, atypical juvenile, BM 1966.430. Arrows indicate first upper labial scales.

Of these features, the following are probably derived, rather than primitive, within the Lacertidae as a whole: 1, 2, 3, 5, 7, 8, 10, 12, 15, 16, 21, 22, 24, 25, 27, 28, 31, 32, 33 and 34. Only number 27 appears to be unique to *Acanthodactylus* but 22, hemipenial asymmetry with the medial side of the organ reduced, is found elsewhere only in *Philochortus* Matschie, 1893 which, on other grounds, does not seem to be closely related. Monophyly is also suggested by (i) the great similarity between the species of *Acanthodactylus* so that they are interconnected by high levels of resemblance; (ii) possession of a unique combination of derived features even if they themselves are not unique to the genus; (iii) a coherent geographical range.

The relationship of *Acanthodactylus* to other lacertids is difficult to judge outside the context of a comprehensive revision of the Lacertidae. Boulenger (1921) suggests that the genus is related to *Latastia* Bedriaga, 1884 but the two share only a couple of the derived features listed above, namely 1 and 33. Most derived features are shared with *Eremias* Wiegmann, 1834 (used in the restricted sense of Shcherbak, 1974, for the Palaearctic species) and *Mesalina* Gray, 1838 (used for the north African and southwest Asian species originally referred to *Eremias*—see Arnold, 1980*b*). *Eremias* shares 1, 2, 3, 7, 8, 14, 15, 16, 28, 32, 33 and often 25 and 34 while *Mesalina* shares 1, 2?, 3, 5, 7, 8, 10, 15, 16, 21, 33 and sometimes 28. More characters need to be examined before it can be decided which of these is likely to be the sister taxon of *Acanthodactylus* or whether this is *Eremias* plus *Mesalina*.

Systematic position of *Eremias guineensis*

Eremias guineensis Boulenger, 1887*a* was described on the basis of a single hatchling, supposedly from 'Brass, Mouths of Niger' (Nigeria). In fact, as Schmidt (1919) has already suggested, this locality is almost certainly erroneous, or the result of accidental transportation, for all the specimens collected since have come from places far to the north of Brass in the Doka and Sudan woodland areas (vegetation classification of Rosevear, 1965) of Nigeria and Ghana (BM(NH) specimens), Niger (Pappenfuss, 1969) and Cameroon. Material from the latter country was described as a separate species, *Eremias benuensis* Monard, 1949 but Pappenfuss correctly synonymized this form with *E. guineensis*. The differences noted by Monard (p. 740) result largely from comparing adult Cameroon animals with Boulenger's description of a single juvenile, as is clearly apparent now that a number of adults are available from Nigeria and other more western localities. The ostensible differences in head and frontal scale proportions and relative head and leg lengths all result from allometric changes during growth, and the supposedly distinctive conditions of the supraocular scales, supraciliary granules and subnasal scale in *E. benuensis* can all be matched in *E. guineensis* from Nigeria. Finally the supposed difference in pattern (six white stripes on dorsum in *E. benuensis* and allegedly five in *E. guineensis* results from an error in Boulenger's description.

Boulenger placed *E. guineensis* in *Eremias* sens. lat. because it has the combination of fine dorsal scaling, keeled subdigital lamellae and nostril separated from the first upper labial scale that this author regarded as diagnostic of the genus. But he felt that this species occupied an isolated position within the assemblage and assigned it to a new subgenus, *Taenieremias* Boulenger, 1918*b*. This separation of *E. guineensis* from the rest of *Eremias* sens. lat. appears valid, for it differs in a number of features from the three main groups included in Boulenger's concept of the genus. It can be distinguished from *Eremias* proper (a Palaearctic assemblage) by having its postorbital and postfrontal bones unfused, by absence of a radially directed peripheral section on scleral ossicle number 14, possession of C-type caudal vertebrae, a reflectable collar and an asymmetrical hemipenis; from members of *Mesalina* by absence of a radially directed peripheral section of scleral ossicle number 14, absence of an occipital scale, possession of three rows of scales around the digits, which are pectinate, and an asymmetrical hemipenis; and from the Ethiopian species usually referred to *Eremias* and the probably related *Meroles* by C-type caudal vertebrae and an asymmetrical hemipenis which differs in detail from any found in that group. It also differs from the great majority of them in its heart-shaped sternal fontanelle and in absence of a peripheral section of scleral ossicle 14 and of an occipital scale.

On the other hand, *E. guineensis* agrees with all the features of *Acanthodactylus* listed on pp. 293–294 with the exception of the arrangement of scales around the nostril (features 26 & 27). Yet even here the situation in *E. guineensis* is not very like that found in species assigned to *Eremias* sens. lat. and in size, shape and pattern of contact with each other, the scales bear a close overall resemblance to those in *Acanthodactylus*, the only obvious difference being the presence of an extra suture in *E. guineensis* running across the area occupied by the first upper labial scale in *Acanthodactylus* to produce a smaller, nominal first upper labial and a subnasal scale that is radically different in form from that found in members of *Eremias* sens. lat. (Fig. 2). Evidence that the *E. guineensis* condition is easily derived from that found in *Acanthodactylus* is provided by a juvenile *A. erythrurus lineomaculatus* (BM(NH) 1966.430) which, although normal in other respects, possesses an extra suture that virtually duplicates the condition found in *E. guineensis* (Fig. 2e).

In addition to possessing the overwhelming majority of the features found in all or most *Acanthodactylus, E. guineensis* bears a more detailed resemblance to *A. boueti* of north Dahomy and Ghana and to *A. erythrurus* and *A. savignyi* of northwestern Africa (p. 318). Given this degree of similarity, it seems best to transfer *E. guineensis* to *Acanthodactylus,* as suggested elsewhere (Arnold, 1980*b*).

Characters varying within *Acanthodactylus*

The following features may vary between species of *Acanthodactylus* and are therefore potentially useful in defining species and in attempting to work out their inter-relationships. Species names mentioned in the course of description are used in the senses employed subsequently in this paper. A summary of many of the features is given in Tables 8 and 9.

Osteological characters

Shape of the premaxillary region (Fig. 3).

In many *Acanthodactylus* the outer edge of the premaxilla (viewed from above or below) is smoothly continuous with those of the maxillae, but in some species this bone is abruptly narrowed and there may be a slight constriction where its lateral surfaces meet the maxillae.

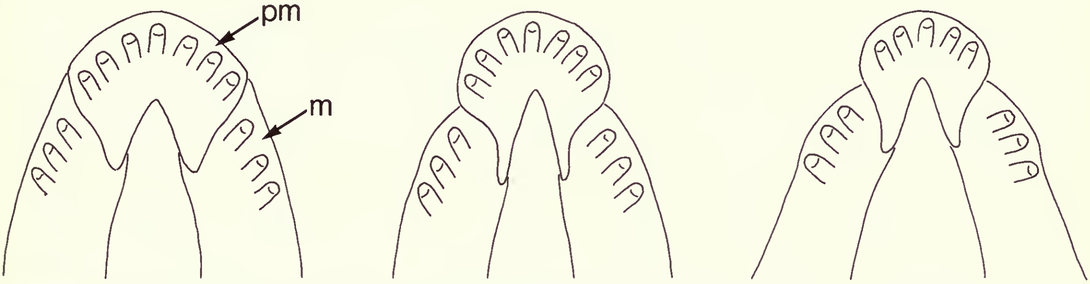

Fig. 3 Premaxillary regions of *Acanthodactylus* skulls from beneath: (left) *A. erythrurus*—outer edge of maxilla and premaxilla smoothly continuous; (centre) *A. schmidti* premaxilla abruptly narrowed; (right) *A. scutellatus*—premaxilla abruptly narrowed and premaxillary teeth reduced to five. pm–premaxilla m–maxilla.

This condition is strongly developed in *A. blanfordii, A. schmidti, A. arabicus, A. gongrorhynchatus, A. haasi, A. masirae* and especially the members of the *A. scutellatus* group: it is at least indicated in many *A. boskianus, A. cantoris* and *A. opheodurus.* A smooth lateral border to the anterior part of the skull is the usual condition in lacertids and the narrowing found in some *Acanthodactylus* is almost certainly apomorphic. It is best developed in species habitually living on soft sand. These forms usually have very acutely pointed snouts and at least some probe the sand when hunting, perhaps in response to tactile or aural cues originating from hidden invertebrates. Narrowing of the premaxilla may be related to producing the acuminate snout-tip necessary for this activity.

Number of premaxillary teeth.

The usual number of premaxillary teeth in most *Acanthodactylus* species is seven with occasional individual variation to six or eight. The three specimens of *A. boueti* checked are singular in apparently having nine premaxillary teeth while many members of the *A.*

scutellatus group have only five; this is true of the great majority of *A. scutellatus* and *A. longipes* examined but of only a few *A. aureus* (see p. 328). As the number of premaxillary teeth in most lacertids is about seven to nine, five seems likely to be an apomorphic condition within *Acanthodactylus*. Its development may well be connected with the narrowness of the premaxilla in these forms.

Postorbital and postfrontal bones.
These elements are separate in nearly all *Acanthodactylus* but they are fused in *A. cantoris*, even juvenile ones.

Number of presacral vertebrae.
There are from 23 to 27 vertebrae between the skull and the sacrum in *Acanthodactylus*. The interspecific variation encountered during this study is set out in Table 1. From this it will be seen that, in most species, males usually have more presacral vertebrae than females, the average difference in vertebral number between them varying from about 0·66 to 1·23. The main exceptions to this are *A. pardalis bedriagai* and members of the *A. scutellatus* group where average sexual differences are very small, ranging from −0·07 to 0·28. Although most populations of *A. schmidti* show sexual differentiation in count, this is very reduced in populations from the United Arab Emirates, eastern Arabia. In the majority of species, there are 24 presacral vertebrae in most males and 25 in most females, but counts are higher in *A.* (*t.*) *tristrami, A.* (*t.*) *orientalis, A. robustus, A. erythrurus, A. savignyi, A. boueti* and *A. guineensis*: here males typically have about 25 presacral vertebrae against usually 26 or even 27 in females. *A. pardalis bedriagai* generally has 26 vertebrae in both sexes while in male and female *A. schmidti* from the United Arab Emirates, *A. scutellatus* and *A. aureus* average counts approach 24; the average is even lower in *A. longipes* and in some parts of its range may be around 23.

Nearly all other lacertids show marked sexual variation in vertebral number, so its reduction is likely to be apomorphic. Counts of 23 in males and 23 or 24 in females are at the lower limit for lacertids as a whole and may well be derived conditions. Other counts are well within the normal range for the family but the higher ones, 25 in males, 26 or 27 in females, may possibly also be apomorphic as they commonly occur only in a minority of forms which on other grounds may be closely related.

In general, species with high presacral vertebral counts are found in relatively mesic habitats while those with low vertebral numbers occur in drier, more open places with sparser vegetation. It may be that the former habitat type requires more body flexion in passing through plant cover and more vertebrae facilitate this. Certainly in lacertids as a whole there is a distinct if imprecise correlation between vertebral number and habitat structure.

The selective pressures that cause loss of sexual differentiation in vertebral number are obscure. Possibly the difference in average count found in most lacertids reflect sex-correlated difference in microhabitat, males might, for instance, spend more time in open situations than females. If this were so, uniformity of vertebral number might result from lack of such microhabitat differences, something that seems quite probable in the relatively uniform, open environments occupied by *A. schmidti* and the *A. scutellatus* group. Another possibility is that the extra vertebrae of most female lacertids increase the length of the body cavity for carriage of eggs and that loss of sexual differentiation is a correlate of small clutch mass. However, although egg number in the *A. scutellatus* group at least is quite small ($n = 2$ or 3) there is no clear evidence that a clutch occupies a smaller proportion of the body cavity than in most other species of *Acanthodactylus*.

Sternal ribs.
In the great majority of *Acanthodactylus* species the usual sternal rib formula is 3 : 2, that is three pairs of ribs attach directly to the sternum and two to the xiphisternum. However, in nearly all of these, the fifth sternal rib is interrupted on at least one side in a minority of individuals, albeit often only briefly. In contrast, interruption is the commoner condition in

Table 1 *Acanthodactylus*: variation in number of presacral vertebrae and incidence of interrupted fifth sternal ribs

	Number of presacral vertebrae									Average difference between males and females	Proportion of animals in which the fifth sternal rib is interupted
	Males				Females						
	23	24	25	26	23	24	25	26	27		
A. micropholis		2					2			1·0	2/2
A. cantoris		*5*					*3*			1·0	1/8
A. blanfordii		*8*	1			1	*7*			0·77	3/16
A. schmidti											
United Arab Emirates	1	*9*			1	*8*	4			0·33	3/18
Others	1	*6*					*6*			1·1	1/10
A. arabicus	1	*8*				1	*7*			1·1	6/14
A. gongrorhynchatus		1				1	1				2/3
A. haasi		1									0/1
A. boskianus		*22*	3		1	5	*13*	1		0·68	4/43
A. schreiberi		*10*				1	*8*	1			3/20
A. grandis complex		*9*					*9*			1·0	5/17
A. (t.) tristrami			5	1				*5*	2	1·13	4/13
A. (t.) orientalis			4					4			2/2
A. robustus			*3*				1		1	1·0	3/5
A. erythrurus		1	*12*				1	*9*	3	1·23	5/28
A. savignyi			*8*					*6*		1·0	
A. boueti			*3*					1	1	1·5	
A. guineensis			*3*					*6*		1·0	0/9
A. pardalis pardalis		*7*	5				*11*	2		0·73	20/24
A. pardalis bedriagae			1	*13*				*6*		0·07	10/18
A. maculatus	3	*29*	4			1	*26*	3		1·04	6/10
A. spinicauda		*7*					*3*			2·0	7/10
A. aureus	1	*9*			1	*8*	1			0·1	19/20
A. scutellatus	6	*30*			3	*45*	9			0·28	62/71
A. longipes	*8*	3			5	2				−0·08	9/11
A. opheodurus	1	6	*4*			2	*11*	1		0·66	4/13
A. felicis		*5*	1				*9*			0·84	0/13
A. masirae		*4*					*2*			1·0	0/5

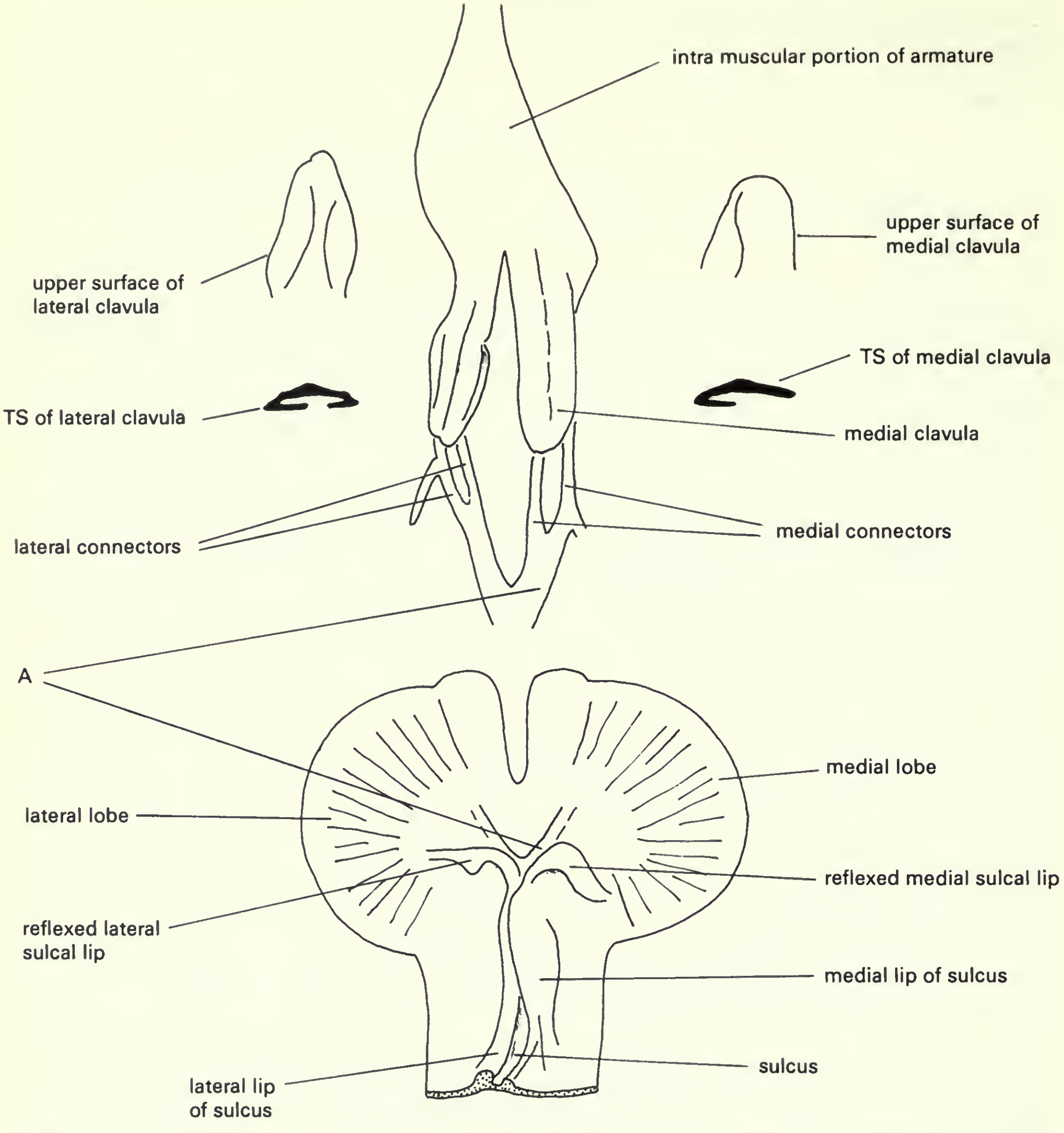
intra muscular portion of armature
upper surface of medial clavula
upper surface of lateral clavula
TS of medial clavula
TS of lateral clavula
medial clavula
medial connectors
lateral connectors
A
medial lobe
lateral lobe
reflexed medial sulcal lip
reflexed lateral sulcal lip
medial lip of sulcus
sulcus
lateral lip of sulcus

Fig. 4 Left armature and unreverted hemipenis of *Acanthodactylus micropholis*, diagramatic view from below, the base of the hemipenis is at the bottom of the illustration. The *m. retractor penis magnus* and ventral wall of the hemipenis have been removed, the flattened hemipenial lobes spread out and the armature disconnected: normally the points marked A coincide, with the armature lying largely above and behind the retracted hemipenis.

members of the *A. pardalis* and *A. scutellatus* groups, sometimes overwhelmingly so (Table 1.) Furthermore, the fifth sternal rib is frequently reduced to quite a small vestige.

Hemipenial characters

Like many other lacertids, *Acanthodactylus* has a hemipenis with an armature, that is a discrete and complex supporting structure of dense connective tissue situated mainly in and around the *penis retractor magnus* muscle. Its basic anatomy and that of the lacertid

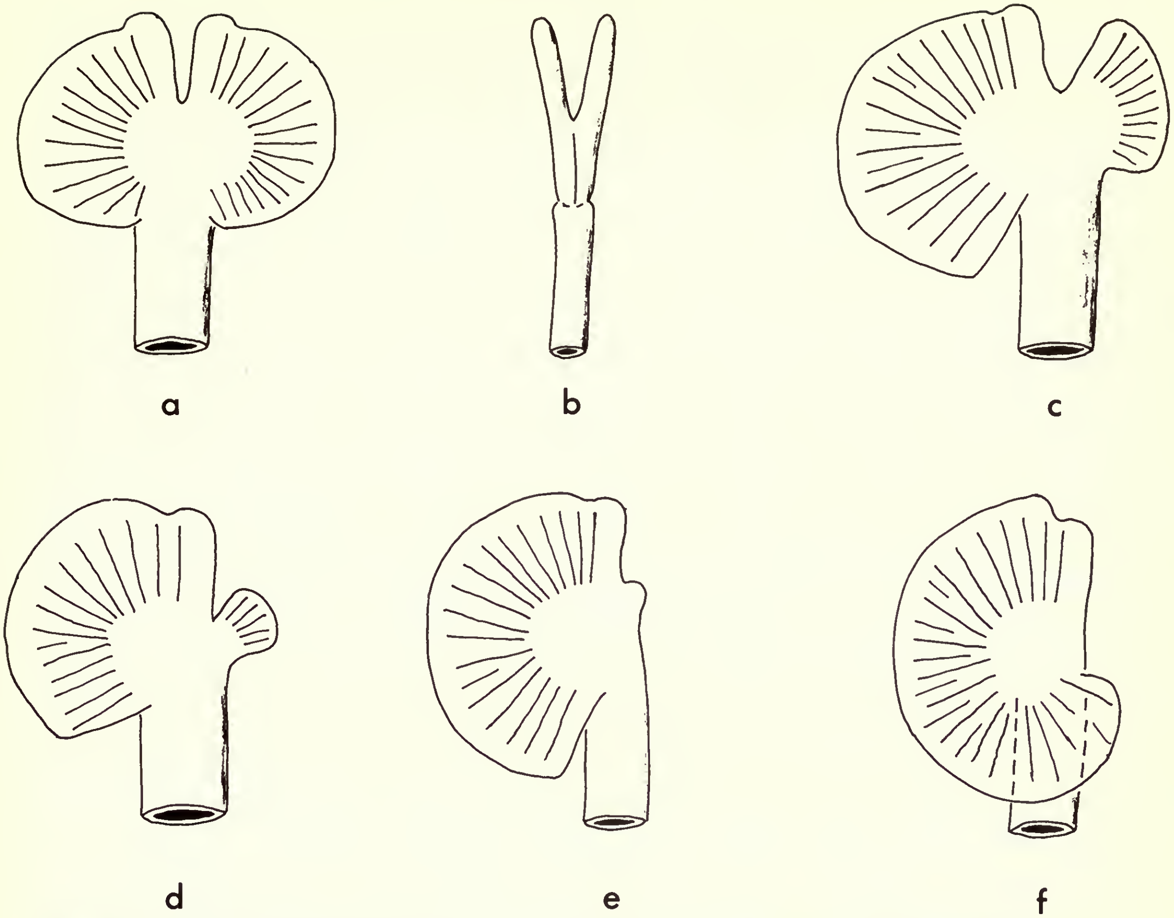

Fig. 5 Uneverted left hemipenes of *Acanthodactylus spp.* showing variation in form and symmetry. In all except (b), the lobes are flattened and normally complexly folded, but they have been spread out for illustration. (a) lobes subequal (*A. micropholis*); (b) lobes subequal but tubular and unflattened (*A. cantoris*); (c) medial lobe somewhat reduced (*A. blanfordii*, *A. pardalis* generally similar); (d) medial lobe very small (some *A.* (*t.*) *orientalis*); (e) medial lobe minute, lateral lobe large (e.g. *A. schmidti*); (f) medial lobe absent, lateral lobe extremely large (e.g. *A. scutellatus*).

hemipenis in general are described elsewhere (Arnold, 1973; and in press) but Fig. 4 shows the salient features in *Acanthodactylus*. A number of variations between species are described below, and are illustrated in Figs 5 and 6.

Size.

Hemipenes are small in *A. cantoris, A. boueti, A. maculatus* and *A. spinicauda.*

Asymmetry in the lobes of the hemipenis.

In many species, the two lobes are subequal in size but in others the medial lobe is reduced while the lateral one increases in size and becomes more fan-like in the uneverted organ. The amount of medial reduction varies and in some cases the medial lobe is absent or minute.

Lobes subequal: *A. micropholis, A. cantoris, A. boskianus, A. schreiberi, A. grandis* complex, *A.* (*t.*) *tristrami, A. robustus, A. erythrurus, A. savignyi, A. boueti.*

Medial lobe somewhat reduced: *A. blanfordii.*

Medial lobe more strongly reduced: *A. pardalis*, some *A. (t.) orientalis.*

Medial lobe very small: some *A. (t.) orientalis.*

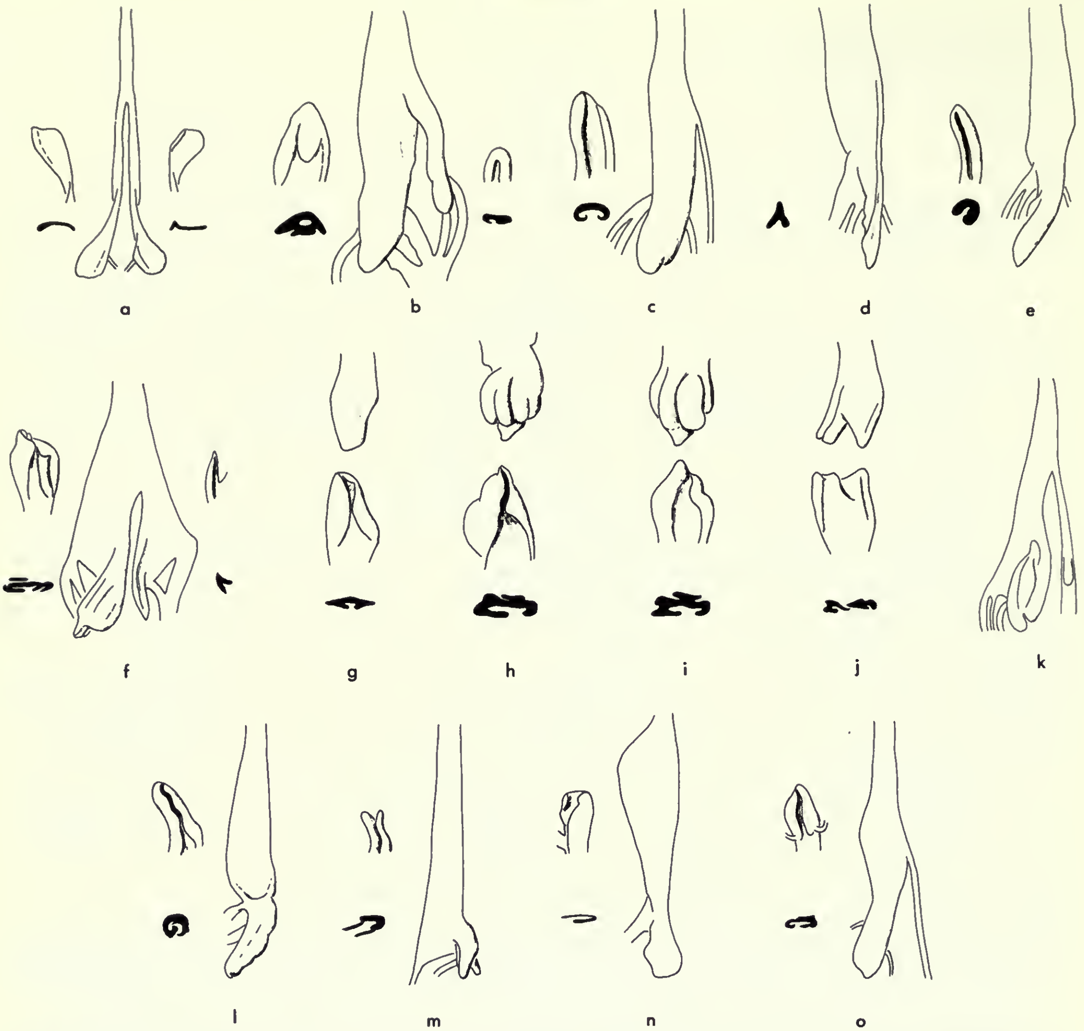

Fig. 6 Left armatures of *Acanthodactylus* species. Main views from beneath; arrangement of distal views of clavulae and of their transverse sections as in Fig. 4: (a) *A. cantoris*: (b) *A. blanfordii*; (c) *A. schmidti*; (d) *A. arabicus*; (e) *A. gongrorhynchattus*; (f) *A.* (*t.*) *tristrami.*

A number of species have generally similar armatures to *A.* (*t.*) *tristrami* but differ mainly in the form of their lateral clavula, consequently in (g)–(j) only this is shown, ventral and dorsal views and a cross section being given: (g) *A. robustus*; (h) *A. grandis*; (i) *A. boskianus*; (j) *A. e. erythrurus, A. pardalis*; (k) *A.* (*t.*) *orientalis*; (l) *A. guineensis*; (m) *A. maculatus*; (n) *A. scutellatus*; (o) *A. opheodurus.*

Medial lobe minute or absent: *A. schmidti, A. arabicus, A. gongrorhynchatus, A. haasi, A. guineensis, A. maculatus, A. spinicauda, A. aureus, A. longipes, A. scutellatus,* and the *A. opheodurus* group.

Lobe shape.
In most *Acanthodactylus,* the hemipenial lobes are flattened and fan-shaped, but complexly folded in the uneverted organ. However, in *A. cantoris* they are narrow and tubular.

Form of the proximal lip of the medial branch of the sulcus.
This is usually well developed and flap-like in species where the medial side of the hemi-

penis is relatively large, although it is usually reduced in forms where this is not so. *A. boskianus, A. schreiberi* and *A. grandis* are exceptional in having a well-developed median lobe but a weak proximal lip to the medial branch of the sulcus.

Reduction of the medial side of the armature.
In most species, the medial side of the armature is reduced in size, simpler in form than the lateral side and indeed may be entirely absent. The extent to which this reduction occurs varies and shows some correlation with reduction of the medial lobe of the hemipenis, although how precise this is varies.

Sides subequal: *A. micropholis,* some *A. cantoris.*

Medial side somewhat reduced: some *A. cantoris, A. boskianus, A. schreiberi, A. grandis* complex, *A. (t.) tristrami, A. robustus, A. erythrurus, A. savignyi, A. boueti, A. pardalis.*

Medial side more strongly reduced: *A. blanfordii,* some *A. schmidti, A. (t.) orientalis.*

Medial side reduced to a thread or absent: most *A. schmidti, A. arabicus, A. gongrorhynchatus, A. haasi, A. guineensis, A. maculatus, A. spinicauda, A. aureus, A. scutellatus, A. longipes, A. opheodurus, A. felicis, A. masirae.*

In these forms the medial branch of the sulcus is short or absent.

Shape of the medial clavula.
In species where a medial clavula is present there are two main patterns.

Clavula fairly broad, flat and blunt-tipped with at least the inner edge turned upwards: *A. micropholis, A. cantoris, A. blanfordii* and some *A. schmidti.*

Clavula narrow and pointed with a ⌣-shaped cross section: *A. boskianus, A. schreiberi, A. grandis* complex, *A.* (*t.*) *tristrami, A. robustus, A. erythrurus, A. savignyi, A. boueti, A. pardalis.*

In *A.* (*tristrami*) *orientalis* the median clavula is like this or very small and flattened.

Shape of lateral clavula.
Substantial differences are found in the form of this structure.

1. Simple, flattened, often with one or both edges turned dorsally: *A. micropholis, A. cantoris,* some *A. schmidti, A. robustus, A. opheodurus, A. felicis, A. masirae.*
2. Not flattened, blunt, edges folded dorsally, a central lobe on the upper surface with a proximally directed pocket: *A. blanfordii,* many *A. schmidti.*
3. Very narrow, hollowed above: *A. arabicus, A. gongrorhynchatus* (*A. haasi* has a similar but shorter lateral clavula).
4. Complexly structured with multiple lobes below: *A. boskianus, A. schreiberi* (most medial lobe often single), *A. grandis* complex (most medial lobe often divided).
5. Complexly structured although not conspicuously lobed below, sometimes very slightly bifurcate: *A.* (*t.*) *tristrami.*
6. Complexly structured and not conspicuously lobed below but clearly bifurcate at tip: *A.* (*t.*) *orientalis, A. erythrurus, A. savignyi, A. boueti, A. pardalis.*
7. Lateral clavula simple but often bifurcate and folded to give a ⊃-shaped cross section: *A. maculatus, A. spinicauda.*
8. Lateral clavula flattened and not bifurcate but folded to give a ⊃-shaped cross section: *A. aureus, A. scutellatus, A. longipes.*

Connectors.
In some species the connectors are all relatively thin but in others the most medial one on the lateral side is usually thickened. This is found in *A. boskianus, A. schreiberi,* the *A. grandis* complex, *A.* (*t.*) *tristrami, A.* (*t.*) *orientalis. A. robustus, A. erythrurus, A. savignyi, A. boueti, A. guineensis, A. pardalis, A. maculatus* and *A. spinicauda.*

Polarity of hemipenial features

The only available criterion for the polarity of hemipenial features found in *Acanthodactylus* is outgroup comparison using other lacertids as the outgroup. In these, the hemipenis is usually fairly large and symmetrical with well developed sulcal lips on both sides. Where present the armature is also typically symmetrical with simple, often flattened and rather blunt clavulae. On this basis, small size, asymmetry of the lobes, sulcal lips and armature and the development of peculiar and often complex clavulae and thickened connectors are all likely to be derived features.

Origin of hemipenial differences

It is common in many animal groups for genital structure to vary between taxa and for at least some of its features to be considered good indicators of relationship, especially as they often correlate with characters from other organ systems. The origin of such differences and possible reasons why they should often reflect relationship are discussed at length elsewhere (Arnold, 1973; in press). It is suggested that genitals differ from other organ systems in their potential to retain changes that develop in them as a result of pleiotropic effects or transient selective forces. With most organ systems, any pleiotropically induced change is likely to result in a loss of functional efficiency. Provided this lowering or efficiency does not outweigh the original selective advantage of the genetic change concerned, the pleiotropic alteration will initially become fixed. But there will then be normalizing selection modifying the genotype so that the pleiotropic change will tend to be suppressed and the organ will return to its original state and level of efficiency. Similarly, if the organ changes in response to direct but transient selective pressure, it will tend to revert to its original condition once this pressure is relaxed.

The situation with genitalia is different since their efficiency cannot be considered in isolation but only in relation to their co-ordinated functioning with the genitals of the opposite sex. Efficiency does not depend on a particular conformation or size but on good match between the sexes. Consequently, if there were, say, a pleiotropic change affecting the male organs which reduces copulatory efficiency, there would not only be normalizing selection acting on the male genotype to bring the male organ back towards its original condition but also, simultaneously, selection acting on the female genotype to produce genital changes adapting to the pleiotropic alterations that have already taken place in the male system. This means that the two sets of genitals might return to their previous mutual efficiency without reverting to their original morphological state. The same sort of effect would be expected if transient selective forces acted directly on the genitalia themselves. Genitals are thus likely to 'store' changes, which in other organ systems would probably be eradicated. So they may be on the whole more likely to incorporate evidence of shared evolutionary experience than many other organs.

An important factor in the production of hemipenial differences in lizards, including *Acanthodactylus,* may be the development of physical isolating mechanisms when previously allopatric species come into contact. Such isolating mechanisms could reduce the loss of reproductive effort which is likely if two species interbreed. That such loss can occur is evidenced by the occasional discovery of hybrids between lacertid species (cases in *Lacerta* and its relatives are summarized by Arnold, 1973, and in *Acanthodactylus* by Mertens, 1968). Physical isolating mechanisms would be at a premium in situations where similar species with no experience of each other come into contact since, in this situation, premating isolating mechanisms may not be well developed. Interspecific mating would be reduced if considerable mismatch evolved in the shape and dimensions of the genitalia of the forms concerned. The often radically different hemipenes of otherwise similar species of *Acanthodactylus* may be examples of this, especially as they correspond in shape and size to the cloacal bursa of their own females into which the male organ is inserted. Such differences occur between forms which, on other grounds, are likely to be closely related, for instance *Acanthodactylus pardalis* and *A. maculatus* and, because they reduce the possibility of successful copulation between the forms, are prima facie evidence of separate species status. Some of the derived features found in the hemipenes of *Acanthodactylus* can be interpreted as contributing to such isolating mechanisms; they include not only small size but also asymmetry of the hemipenis and armature since loss of its medial side reduces the diameter of the organ.

Although they are likely to be 'stored' beyond their period of function (presumably premating isolating mechanisms are likely to develop in the long run), changes that are probably associated with physical isolating mechanisms are not likely to be very reliable indicators of relationship. This is partly because, by their nature, they tend to produce marked differences between very similar and often closely related species. Also, means of producing incompatible genitalia are rather restricted in lizards and it is very likely that small size and asymmetry may have been produced several times. This is supported by their patchy occurrence in *Acanthodactylus,* turning up in a number of groups which on other grounds do not seem to be closely related. Furthermore these features have developed in other lacertid genera. Other hemipenial features may not be subject to such strong convergent selective forces and, as such are more likely to be good indicators of relationship for the reasons given earlier in this discussion.

Description of the hemipenes of different species

Figures in parentheses refer to the number of individual organs examined.

A. micropholis (2). Lobes more or less symmetrical or medial rather reduced, sulcus bifurcate, the proximal borders of its branches formed by backwardly directed flaps; armature fairly symmetrical although one or other clavula larger than the other, clavulae rather expanded and obtusely pointed, the medial one with its inner edge turned upwards, lateral one with both edges turned upwards; often three lateral connectors and two medial ones, all narrow.

A. cantoris (7). Size reduced; medial lobe usually rather smaller than lateral, lobes not complexly folded, the walls often corrugated and lack regular plicae, stem of hemipenis long, sulcus bifurcate, the proximal borders of its branches formed by a soft flap in at least some cases although this is not always clear; armature symmetrical or medial side somewhat reduced, slender, the clavulae expanded and laminar, medial with inner edge turned upwards, lateral with both edges turned upwards, at least one connector on each side.

A. blanfordii (10). Lateral lobe large and medial one reduced, sulcus bifurcate, proximal border of lateral but not medial side formed by a backwardly directed flap; armature clearly asymmetrical, the median side reduced with a flattened clavula of which the inner edge is turned upwards, lateral clavula large and obtusely pointed, not flattened, edges turned upwards and a central lobe present on the upper side below which there is a proximally directed pocket (the lobe is least developed in southern populations), connectors as in *A. micropholis.*

A. schmidti (10). Lateral lobe large and fan-shaped, medial lobe absent or minute, sulcus bifurcate but medial branch very short; medial side of armature absent or reduced to a thread in most cases; lateral clavula large, either rather pointed, slightly bifurcate or rather blunt, edges turned upwards and clavula may be rolled to some extent, a central lobe present in many cases on the upper side, below which is often a proximally directed pocket as in *A. blanfordii* but is less well developed. In one case (BM(NH) 1931.7.16.48) there is a flattened medial clavula.

A. arabicus (6). Essentially like *A. schmidti* but intramuscular part of armature much narrower and lateral clavula very narrow, simple and pointed with a concavity above or the medial edge rolled upwards.

A. gongrorhynchatus (1). Similar to *A. arabicus* but medial edge of clavula rolled onto dorsal surface.

A. haasi (1). Like *A. gongrorhynchatus* but clavula shorter, broader and more dorso-ventrally flattened.

A. (*tristrami*) *tristrami* (3). Lobes more or less symmetrical, sulcus bifurcate, the proximal borders of its branches formed by distinct flaps; armature asymmetrical, the medial side reduced with a pointed clavula that has a ≺-shaped cross section; lateral clavula expanded and, when spread out, essentially flat with a very weakly bifurcate tip formed of overlapping laminae, lower surface fairly smooth but with a strap-shaped area with free edges towards outer side, upper surface with a medially directed pocket and edges rolled upwards; three lateral and two medial connectors, the more medial of the lateral ones thickened.

A. (*tristrami*) *orientalis* (4). Different from *A.* (*t.*) *tristrami:* lateral lobe very large and medial strongly reduced (as in Fig. 5c or d), sulcus bifurcate, proximal borders of branches formed by distinct flaps, the median one rather small; armature very asymmetrical, medial clavula quite small, either pointed with a ≺-shaped cross-section or blunt and flattened; lateral clavula rather similar to that of *A.* (*t.*) *tristrami* and has free strap-shaped area on lower surface but is smaller with a more bifurcate tip and no clear pockets.

A. robustus (2). Generally like *A.* (*t.*) *tristrami* but lateral clavula much simpler with edges turned on to dorsal surface.

A. boskianus (10), *A. schreiberi* (5). Generally like *A.* (*t.*) *tristrami* but proximal border of medial branch of sulcus is a relatively weak, soft fold rather than a flap; lateral clavula has similar general form but is more swollen and lobed and there is an area with free edges towards the medial side of the ventral surface; upper surface has medial edge rolled upwards and greatly swollen. In *A. schreiberi* and *A. boskianus* the median area of the ventral surface may be divided by a longitudinal cleft.

A. erythrurus erythrurus (3), *A. e. lineomaculatus* (3), *A. savignyi savignyi* (2), *A. s. blanci* (2). Similar to *A.* (*t.*) *tristrami* but lateral clavula usually clearly bifurcate at tip and the more median cleft in *A.* (*t.*) *tristrami,* that separates a strap shaped area with free edges in this form, is usually not clearly marked.

A. e. belli (6). As *A. e. erythrurus* but lateral clavula is smaller, flatter and usually simpler.

A. boueti (1). Size reduced; lobes subequal; armature asymmetrical, the medial side reduced with a pointed clavula that has a ≺-shaped cross section; lateral clavula expanded and flattened, bifurcate at tip, with lateral edge turned upwards.

A. guineensis (1). Lateral lobe very large, medial lobe absent, sulcus lacks medial branch, proximal border of its lateral branch formed by a backwardly directed flap; medial side of armature absent, lateral clavula superficially narrow but in fact laminar and tightly rolled, lower surface smooth but with a cleft near each margin, dorsum with a medially directed pocket; two connectors, the more medial one broad.

A. pardalis (20). Lateral lobe large and medial small but plicate, sulcus bifurcate, the proximal border of its branches formed by backwardly directed flaps; armature very like that of *A. erythrurus* and *A. savignyi.*

A. maculatus (20), *A. spinicauda* (2). Small; lateral lobe large, medial lobe absent; medial branch of sulcus very short, proximal border of lateral branch only of sulcus formed by backwardly directed flap; medial side of armature absent or reduced to a thread, lateral side narrow and clavula small but sometimes bifurcate; compared to condition in *A. pardalis,* lateral clavula has been rotated and folded to give a ⊃-shaped cross section so that the bifurcation, if present, is in the vertical plane; two or three connectors, the most medial one usually thickened.

A. aureus (3). Lateral lobe large and fan-shaped, medial lobe absent or very small and confluent with lateral one, medial branch of sulcus absent or very short; medial side of armature absent or reduced to a thread, lateral side broad; lateral clavula flattened but rotated sideways, as in *A. maculatus,* and folded to give a ⊃-shaped cross section, with two connectors.

A. scutellatus (5), *A. longipes* (3). Generally similar to *A. aureus* but folded clavula usually broader and sometimes apparently only one connector present.

A. opheodurus (10), *A. felicis* (4), *A. masirae* (2). Lateral lobe extremely large, medial one very reduced, sulcus with relatively short medial branch, proximal border of lateral branch usually visible as a rather weak flap or fold; medial side of armature reduced to a thread or absent, lateral clavula usually flattened with the margins rolled over onto dorsal surface; lateral connectors usually two or sometimes three, slender.

External features

These have nearly all been used by Boulenger (1918*a*, 1921) and subsequent authors and, until now have formed the basis of *Acanthodactylus* classification.

Scales around nostrils.
A. guineensis has a peculiar perinasal scale arrangement that seems to be derived from the typical *Acanthodactylus* condition, it also occurs as a rare variant in *A. erythrurus* (see p. 296).

Frontonasal scale.
This is usually intact but is frequently divided in two by a longitudinal suture in some populations of *A. erythrurus* and *A. savignyi.* The condition occurs as a rarity in a few other species.

Azygos scales between prefrontals.
One or more azygos scales between the prefrontals occurs commonly in *A. boueti, A. savignyi* and in some populations of *A. erythrurus.* This arrangement is also found as an uncommon variant in *A. guineensis, A. schreiberi* and *A. boskianus* and even more rarely in some other forms.

Supraocular scales.
There is considerable variation in the extent to which the supraocular scales roofing the orbit are fragmented in *Acanthodactylus.* 1. *A. schreiberi* has four large, more or less intact scales; this condition is approached by members of the *A. grandis* complex. 2. In the *A. cantoris, A. scutellatus* and *A. opheodurus* groups and in *A. gongrorhynchatus, A. haasi* and many *A. boskianus* there is usually an area of granules wedged between the third and fourth supraoculars and, in some cases, between the first and second too; the fourth supraocular may also be broken up, at least to some extent. *A. boskianus* from north Egypt and *A. haasi* may have the first supraocular divided into two or three sections. 3. Members of the *A. pardalis* group have the first supraocular sometimes divided into two or even three and the fourth is very fragmented. 4. In the *A. tristrami* and *A. erythrurus* groups the first supraocular is divided into at least three sections and often into many granules and this usually applies to the fourth too. 5. *A. boueti* has the first, second and third supraoculars all fragmented. There is however a significant amount of variation within taxa.

It is probable that the plesiomorphic condition is four more or less undivided supraocular scales, as this is by far the commonest state in the Lacertidae as a whole, but fragmentation seems to have occurred independently in some forms assigned to *Eremias* and in *Ichnotropis.*

Subocular scale.
A number of species have a subocular scale that extends ventrally to the edge of the mouth, separating the, in these cases, usually four anterior upper labial scales from the remainder. This condition is found in *A.* (*t.*) *tristrami, A.* (*t.*) *orientalis, A. masirae, A. boueti* and *A. guineensis,* in many *A. micropholis, A. erythrurus* and *A. savignyi,* in a few *A. boskianus* from the Iraq region and in occasional examples of some other species such as members of

the *A. pardalis* group and *A. opheodurus*. Elsewhere the subocular is shallower and the upper labials form a continuous series beneath it. The former state is likely to be plesiomorphic as it is very widespread in the Lacertidae as a whole, but the latter occurs in *Eremias* proper, in some species usually assigned to *Eremias* from the Ethiopian region and in *Meroles* Gray, 1838, *Aporosaura* Boulenger, 1887*b* and *Ichnotropis* Peters, 1854. The supposed apomorphic condition may apparently arise by the subocular becoming increasingly narrowed ventrally or by splitting to produce a small ventral scale that forms an extra upper labial.

In general, the subocular is separated from the lip in forms from drier, more open habitats which tend to have particularly large eyes and the character may be at least partly a functional correlate of this size increase. In species where the subocular scale usually borders the mouth, the lateral surface below the anterior eye, formed from the jugal and maxillary bones, tends to be fairly vertical, so that the scale can cover it but still remain roughly in the same plane as the upper lip of which its lower section forms part. But, with increase in eye size, the jugal arch bulges outwards and its outer face and that of the section of the maxilla below it is directed more obliquely downwards. In this situation, a single scale covering this surface and forming part of the lip would be strongly bent and possibly not able to provide the necessary flexibility for labial movement. In forms living in dry areas, the need for such movement is increased, for the upper lip projects further ventrally and is more bulky, so it and the scales covering its outer surface are displaced more during closure of the mouth, presumably producing a more efficient seal against water loss and incursion of sand particles than is present in more mesic species. Because of these changes, the replacement of the original subocular by two functional parts would probably be an advantage.

Number of upper labial scales anterior to the centre of the eye.
In the majority of forms there are typically four upper labials anterior to the centre of the eye but in some, such as the members of the *A. cantoris* group, *A. scutellatus* and *A. longipes,* five is the usual number. As four is found in forms which on other grounds seem primitive, it may be the plesiomorphic condition for *Acanthodactylus.* When present, the extra upper labial sometimes seems to develop by being split off the subocular but this may not always be its origin. In many species exceptions to the usual number occur.

Parietal scales.
A. boueti is singular in having the parietal scales reduced and the areas normally occupied by their lateral and posterior parts replaced by small scales.

Ear opening.
This is usually quite large but in *A. gongrorhynchatus* and *A. haasi* it is reduced in size, being occluded by skin from above and from the front. Similar reduction is found in some other lacertids that live on loose sand such as *Aporosaura* and some species of *Meroles.*

Dorsal body scales.
There is great variation in size and shape of the dorsal scales. In many species they are fine and more or less granular and either smooth or carinate, but in others size increases posteriorly and the scales become flat, more keeled and strongly imbricate. In such cases, the lateral scales tend to be smaller than the more medial ones. Transverse counts at mid-body may be as high as 100 in the most fine-scaled species, *A. longipes,* or as low as 18 in some *A. boskianus asper.* There is often substantial variation within and, more obviously, between populations of a species; thus counts vary from about 35 to 80 in *A. scutellatus* and from 18 to 52 in *A. boskianus.* This suggests that dorsal scalation is very labile so that the assessment of a primitive condition for the genus is impossible. All that can be said is that the extremes encountered in *Acanthodactylus* are near the extremes for the Lacertidae as a whole and that the primitive condition is perhaps more likely to be somewhere in between.

In some other sections of the Lacertidae, relatively fine granular scaling is usually associated with open environments while, large, keeled, strongly imbricate scales are typically found in species that live, or at least take refuge in, dense often spiny vegetation.

The latter scale arrangement provides much better mechanical protection against damage to the flexible skin between the scales, something that is potentially likely to occur when running in densely vegetated habitats. The same selective pressure may well act on *Acanthodactylus*; the most fine-scaled forms, like many populations of the *A. scutellatus* group, tend to live in the most open habitats, whereas forms like *A. boskianus* do frequently seem to take refuge in spiny vegetation (see p. 315).

Dorslateral tracts of enlarged scales.
These are found on the posterior body of *A. schmidti* and are at least indicated in some *A. blanfordii.*

Ventral scale number.
The number of ventral scales in the longest transverse row across the belly varies from about 8 to 18, 10 being the commonest figure. As the majority of lacertids have low numbers, these are likely to be primitive in *Acanthodactylus.* In general low numbers are most frequent in forms occupying more mesic habitats and higher ones in species living in relatively arid areas, but this correlation is imprecise. Intraspecific variation occurs, especially in forms with higher counts.

Tessellation of ventral scales.
Forms with high transverse counts of ventrals often have the scales tessellated, that is, they are staggered so that they do not form regular longitudinal rows. In many cases, this staggering is confined to the sides of the belly, but it may affect the median areas too. It is best and most extensively developed in most populations of the *A. scutellatus* group and in the *A. grandis* complex; it is found to a lesser extent in other members of these assemblages and is at least indicated in the *A. cantoris* group and *A. gongrorhynchatus.* There is significant variation in the extent of staggering within species where it is present. Tessellation is found in some other lacertid groups such as *Eremias* proper, *Meroles* and *Aporosaura.*

Intergradation of dorsal and ventral scales.
In most *Acanthodactylus*, dorsal and ventral scales are easily distinguished from each other, but in *A. gongrorhynchatus* they intergrade. This trend is also apparent in *A. haasi* and to a lesser extent in some *A. arabicus.*

Number of rows of scales running along fingers.
In many species there are three rows of scales running along fingers one to four, the same number that runs along each toe. One row is dorsal, one ventral and the third posterior. On finger five, and sometimes at the base of the others, there may be four rows, the additional one being anterior. In contrast, a number of forms have four regular and continuous rows of scales on all fingers; these include the *A. cantoris* and *A. scutellatus* groups, the *A. grandis* complex, *A. gongrorhynchatus* and *A. haasi.* In fact, these two conditions are not as clear cut as they appear, for a number of individuals of species that usually have three scale rows possess additional scales forming an irregular fourth row on at least some fingers; this occurs in *A. micropholis, A. robustus* and *A. opheodurus. A. masirae* habitually has four rows but these are often irregular, and *A. cantoris* in which four regular rows are usually present occasionally has the anterior one strongly reduced.

It seems likely that three scale rows running along the fingers is the primitive condition in *Acanthodactylus* for it comes closest to the two rows typical of the majority of Lacertidae and other scincomorph lizards. Three or four scale rows on the fingers also occur in *Eremias* proper, *Meroles* and *Aporosaura.* The presence of a regular fourth row is largely associated with sandy habitats. It may well allow better development of a pectination on the anterior face of the digit that matches the posterior one. This results in a wider digit that is more efficient for digging in light, unconsolidated substrates such as fine sand where *Acanthodactylus* often scrabbles for food as well as excavating burrows.

Pectination of the digits.

The scales along the posterior surfaces of the digits are pointed and project to form a comb-like fringe or pectination. In some instances, this is inconspicuous but in others the scales become very long and flattened in the horizontal plane and in extreme cases, such as *A. longipes,* the fringe on the toes may be wider than the digits themselves. The scales forming the row running along the upper surfaces of the digits may project slightly forwards to produce a weak anterior fringe as well, but in species where there is an anterior scale row on the fingers, this may form a fringe approaching the posterior one in development.

There is a continuum between the weakest fringes and the most pronounced ones. Degree of development correlates very closely with what is known about the ecology of the species concerned, being least in forms living on relatively hard ground and greatest in forms from soft sand. The relationship is so strong in taxa for which some ecological information is available that it seems reasonable to use degree of pectination to predict substrate type in cases where this is unknown. The importance of fringes on the fingers for digging in loose sand has already been mentioned; fringes also enable lizards to travel across soft sand surfaces efficiently by increasing the area covered so that unit pressure is low and effort is not wasted pushing the sand backwards as the lizard moves forwards.

Keeling on upper caudal scales.

Most *Acanthodactylus,* like the majority of lacertids, have keels on the dorsal scales of the tail base but these are absent in *A.* (*t.*) *tristrami, A.* (*t.*) *orientalis* and *A. robustus.* The restricted distribution of this feature in the Lacertidae suggests it is an apomorphy, although it has developed independently elsewhere, for instance in *Mesalina rubropunctata.*

Lateral processes on tail base.

In *A. spinicauda* the lateral scales at the base of the tail are greatly enlarged, especially in males, with their keels produced to form tubercles. This feature is unique in the Lacertidae.

Tail length.

In most *Acanthodactylus* the tail is more than 1·5 times the length of the head and body together but in *A.* (*t.*) *tristrami, A.* (*t.*) *orientalis* and *A. robustus* it is less.

Pattern.

In the great majority of *Acanthodactylus* species, juveniles have a striking pattern of narrow, dark and light longitudinal stripes. The only certain exceptions are *A. schmidti, A. longipes* and some *A. scutellatus* in which the newly hatched young are uniform or dappled. This condition is likely to be derived as striped patterns are very widespread among juvenile lacertids. When present, the number of dark stripes varies considerably and there may be as many as six pairs, although not all these run the whole length of the body. In the nomenclature of Lantz (1928), developed for Palaearctic *Eremias,* these are 1. the *spinal* originating near the mid-line and usually fusing to produce a single stripe on the body, 2. the *occipital* arising from the hind edge of the parietal scale, 3. the *parietal* arising from the lateral edge of that scale, 4. the *temporal* beginning behind the eye and passing over the upper edge of the ear (equivalent to Lantz's upper and lower temporals), 5. the *maxillary* passing through the ear and 6. the *costal* passing below it.

It is usually acknowledged that a high number of stripes is plesiomorphic in the Lacertidae (Eimer, 1881; Boulenger; 1921; Lantz, 1928) and this condition is certainly commoner in forms which on other grounds seem primitive. Reduction in number seems to take place most usually by loss or fusion of bands at the mid-line. As we have seen, a few *Acanthodactylus* have a pair of spinal bands on the neck that fuse on the body; reduction from this state appears to follow a clear sequence: 1. the spinals fuse throughout their length; 2. the resultant composite stripe shortens while the occipital stripes fuse posterior to it; 3. the spinal stripe is reduced to a vestige or disappears and fusion of the occipitals extends forwards; 4. the occipitals fuse completely to produce a simple mid-line stripe. This means of course that mid-line stripes in *Acanthodactylus* are not always homologous as they can be composed either of fused spinal bands or of occipitals. There may also be loss of the outermost bands, especially the costals on the body.

Presence of a pair of spinal stripes on the neck is largely confined to some *A. micropholis, A. erythrurus* and *A. pardalis.* The partial development of a mid-dorsal stripe made up of the occipitals occurs in some individuals of the following species: *A. boskianus, A. schreiberi, A. pardalis, A. scutellatus, A. opheodurus, A. felicis* and *A. masirae,* but complete fusion seems to be confined to some *A. boskianus* and *A. scutellatus* and most *A. opheodurus.*

A. micropholis retains a simple striped pattern throughout life. In other forms this is often modified, but predominantly striped individuals, or ones with longitudinal rows of spots, are common in most species. However not all the stripes present in juveniles may be discernible in these adults.

A. pardalis and *A. maculatus* are singular in that some individuals of each have spots of brownish red pigment on their backs that do not fade or disappear in alcohol.

In *A.* (*t.*) *tristrami, A.* (*t.*) *orientalis* and *A. robustus* some individuals have two rows of large ocellar markings along the back.

Species boundaries and species groups

The introduction of osteological and especially hemipenial characters provides a partial test of the homogeneity of the species presently recognized within *Acanthodactylus.* For even if the external features on which these nominal taxa are based show little obvious variation, discontinuity in characters from the new sources may indicate that more than one form is involved. The species are mostly discussed below in groups that consist of species with a high level of overall similarity and which, in most cases, probably form holophyletic assemblages, although there are exceptions.

A. micropholis

A. micropholis Blanford, 1874*a,* occurs in southeast Iran and southwest Pakistan, in the latter country occupying sandy places along water courses in hilly areas (Minton, 1966). It has a high proportion of primitive features including the following: premaxilla with about seven teeth and not abruptly narrowed, 24 presacral vertebrae in males and 25 in females, sternal ribs usually intact; hemipenis and armature fairly symmetrical, clavulae flattened and simple, connectors slender; subocular often reaching mouth, frequently four upper labials anterior to centre of eye, eight or ten ventrals in longest row across belly, ventrals arranged in straight longitudinal rows, usually three longitudinal rows of scales on fingers, pectination on digits rather weak, upper caudal scales keeled, young with numerous dorsal stripes which are retained by adults. On the other hand, the first and fourth supraoculars are broken up and, in some individuals, the subocular may be separated from the mouth, five upper labials are sometimes present anterior to the centre of the eye and there may be indications of a fourth scale row on the fingers.

The *A. cantoris* group, *A. gongrorhynchatus* and *A. haasi*

A. cantoris Günther, 1864*b*: NW. India, Pakistan, E. Afghanistan.
A. blanfordii Boulenger, 1918*a*: S. Afghanistan, SW. Pakistan, SE, Iran, Oman (Muscat area).
A. schmidti Haas, 1957: Arabia except extreme west; SW. Iran (Anderson, 1963, 1974).
A. arabicus Boulenger, 1918*a*: SW. Arabia.
A. gongrorhynchatus Leviton & Anderson, 1967: E. and SE. Arabia.
A. haasi Leviton & Anderson, 1967: E. Arabia (Dhahran).

The first four forms, which constitute the *A. cantoris* group, are all associated with loose sand habitats (*A. cantoris*—Minton, 1966; Mertens, 1969, *A. blanfordii*—Blanford, 1874*b*; Anderson, 1963; Clark *et al.*, 1969; M. D. Gallagher, pers. comm. *A. schmidti*—Anderson, 1963; personal observations, *A. arabicus*—Anderson, 1895). Soft ground types are also suggested by the extensive pectination of the digits. Members of the *A. cantoris* group share the following features: premaxilla with about seven teeth and usually abruptly narrowed (least in *A. cantoris*), usually 24 presacral vertebrae in males, 25 in females (less sexual differentiation in some populations of *A. schmidti*), fifth sternal rib often intact; hemipenis and armature usually showing marked asymmetry (not in most *A. cantoris*), clavulae not very complex, connectors relatively slender; first supraocular intact or not much divided and the fourth large or rather fragmented with a group of granules wedged between it and the third, subocular nearly always separated from the mouth, usually five upper labials anterior to the centre of the eye, posterior dorsals coarse and carinate, 12–18 ventrals in longest row across belly, ventrals arranged in fairly straight longitudinal rows, although sometimes staggered at sides, nearly always four longitudinal rows of scales on fingers (anterior row sometimes reduced in *A. cantoris*), pectination on digits strong, upper caudal scales keeled, young usually with numerous dorsal stripes (not in *A. schmidti*) that are typically lost in adults.

In the past it has been usual to treat these four forms as subspecies of *A. cantoris*. But,

Table 2 Variation in the *A. cantoris* group

	A. cantoris	*A. blanfordii*	*A. schmidti*	*A. arabicus*
Hemipenis				
size	small	large	large	large
medial lobe	unreduced	somewhat reduced	minute or absent	minute or absent
medial side of armature	virtually unreduced	somewhat reduced	usually absent	absent
lateral clavula	flat and simple	lobed and pocketed	lobed and sometimes pocketed	very narrow
Postorbital and postfrontal bones	fused	separate	separate	separate
Sexual variation in number of presacral vertebrae	yes	yes	not in populations from United Arab Emirates	yes
Dorsal scales across mid-body	26–36	30–46	33–51	27–35
Dorsolateral tracts of enlarged scales on hind back	no	indicated in some cases	yes	no
Number of ventral scales in longest row across belly	12(14)	(11)12–14(16)	13–18	(12)14–16
Juveniles with dorsal stripes	yes	yes	no	yes
Adults striped or with rows of dark spots	sometimes	sometimes (all animals from Muscat)	no	in west of range
Tail with transverse bands	no	no	in juveniles and many adults	no
Maximum size within populations (snout-vent, mm)	77	60–75	67–105	55–63

although they have a strong overall resemblance to each other and, so far as is known, are allopatric, each has a number of distinctive characters that are often more pronounced than those separating accepted species of *Acanthodactylus* (see Table 2). Because of this, it seems more consistent to give them full species status.

A. cantoris is widespread in northwest India and in Pakistan is found in the southeast and in the Indus drainage whence it reaches east Afghanistan (Kabul River area, CAS 96200–01, 120358–60); it also extends westwards along the Pakistan coast at least to Ormara (BM(NH) 1904.12.7.2; Minton, 1966, records *A. blanfordii* from this locality but his specimens, RSM 1964.58.2/6, are in fact *A. cantoris*). There is some geographical variation, for instance in the Punjab the anterior row of scales on the fingers is incomplete in some animals. This is true of a female from Cambellpur (BM(NH) 1933.5.16.8) which is also peculiar in having a rather blunt snout and elongate, strongly overlapping dorsal scales.

A. blanfordii reaches its easternmost limit in the Helmand drainage of south Afghanistan and the neighbouring border area of Pakistan (BM(NH) 86.9.21.77–80; Mertens, 1969; it is also probable that the specimens listed by Clark *et al.,* 1969, and Minton, 1966 are *A. blanfordii*). *A. blanfordii* and *A. cantoris* may be separated by intervening high ground in this area but it is possible that they meet on the coast for *A. blanfordii* extends eastwards as far as Pasni (Mertens, 1969), only about 130 km from the nearest known *A. cantoris* locality. The differences in dorsal and gular scale counts on which these two forms were originally separated do not always hold but they can be distinguished by the fusion of postorbital and postfrontal bones in *A. cantoris* and by hemipenial features. *A. blanfordii* extends into eastern Iran at least as far as the Bandar Abbas region (Anderson, 1963) and an isolated population has recently been found by M. D. Gallagher near Muscat, southeast Arabia (BM(NH) 1973.723–26, 1976. 1462–64, 1977.68–69); here all the adults examined retain at least traces of dorsal striping.

A. schmidti is widespread in Arabia where it shows substantial regional variation in body size (Arnold, 1981*b*). It also extends into southwest Iran (Anderson, 1974) but without apparently contacting *A. blanfordii.*

A. arabicus is restricted to the littoral area of southwest Arabia and seems to be separated from *A. schmidti* by hilly, not very sandy country occupied by such species as *A. boskianus, A. felicis* and *A. opheodurus.* Although *A. arabicus* and *A. schmidti* both have the medial side of the hemipenis and armature very reduced, they differ in their other apparent apomorphies (*A. arabicus*—very narrow clavula; *A. schmidti*—often very large size, dorsolateral tracts of enlarged scales on hind back, lack of stripes in juvenile and adult patterns) and in dorsal scale number. In fact *A. arabicus* is more similar to *A. blanfordii,* especially Muscat specimens, differing mainly in its more slender build, greater hemipenial asymmetry, narrower clavula and higher number of ventral scales across the belly (usually 14–16 as against 11–13(14) at Muscat). *A. arabicus* from Aden and its vicinity are comparatively large and usually retain stripes or spots when adult but animals from futher east (as far as Gischin (= Qishn), NMW 11814/1–16) are smaller and often become uniform in colouring with maturity.

Relationships within the *A. cantoris* group are not easy to discern with great certainty, since most of the apomorphies available for judging affinities are rather weak (see p. 324), but *A. blanfordii, A. schmidti* and *A. arabicus* all differ from *A. cantoris* in their more narrowed premaxillae, more asymmetrical hemipenes and usually higher number of ventrals, while lacking its fused postorbital and postfrontal bones and its hemipenial peculiarities (p. 305), so they may well form a distinct unit with *A. blanfordii* as the least modified species. Within it, *A. schmidti* and *A. arabicus* share almost total loss of the medial side of the hemipenis and armature, but there are no other apparent synapomorphies joining them, apart from increase in ventral scale count. As extreme hemipenial asymmetry has developed a number of times within *Acanthodactylus,* its value as an indicator of relationship is quite low. It is possible that *A. schmidti* is the sister species of *A. blanfordii* for the latter occasionally shows indications of the dorsolateral tracts of enlarged scales on the hind-back that are typical of the former and they often share a peculiar lateral clavula shape in which there is a proximally directed pocket. Moreover, *A. schmidti* occasionally has a medial clavula exactly like that of *A. blanfordii*. Certainly *A. arabicus* and *A. schmidti* are more like *A. blanfordii* than like each other and may well have been independently derived from a *A. blanfordii*-like stock.

A. gongrorhynchatus is sympatric with *A. schmidti* in east and southeast Arabia and shares many features of the *A. cantoris* group but it differs in its very slender adult build, convex pileus, short but abruptly acuminate snout, weakly keeled supratemporal scales that are fragmented posteriorly, four upper labials anterior to the centre of the eye, an ear hole that is reduced in size and fine dorsal scaling that sometimes grades into the ventral scales. Recent observations by Mr W. Ross (personal communication) show that *A. gongrorhynchatus* lives on aeolian sand. Its morphology—depressed fingers, strong digital pectination, very pointed snout and partly occluded ear opening—is appropriate for such a substrate and suggests that it is more strictly confined to this habitat than *A. schmidti* which occupies the same general area. *A. gongrorhynchatus* may well be paedomorphic in some features which are typical of juvenile *Acanthodactylus,* for instance the rounded pileus, short snout and lack of strong keeling on the supratemporal scales. In fact it has substantial resemblance to immature specimens of *A. arabicus* and may well be closely related to this species, especially as their hemipenes are very similar including the very narrow lateral clavula.

The present situation in Arabia may have arisen by a second stock of the *A. cantoris* group invading to exist alongside one already present. It is possible that much of the peninsula was originally occupied by *A. arabicus*-like populations and that the precursor of *A. schmidti* entered the area from the east to become sympatric with them, except in the extreme southwest littoral region which is isolated by geographical barriers. Here *A. arabicus* survives but elsewhere coexistence of two species in soft-sand habitats favoured by the *A. cantoris* group would be expected to produce considerable character displacement, the *A. arabicus*-like stock giving rise to *A. gongrorhynchatus* and the invading one to *A. schmidti,* the two most divergent species in the assemblage. An analagous situation exists among the nocturnal ground geckoes of the genus *Stenodactylus* that occupy soft sand habitats (Arnold, 1980*a*). As in *Acanthodactylus* there is a single species in the southwestern littoral region of Arabia (*S. pulcher*) which has a close relative widespread in the peninsula (*S. arabicus*), where it is sympatric with another more distantly related species (*S. doriae*). As with *A. gongrorhynchatus, S. arabicus* is more strongly adapted to sandy environments and smaller than its southwestern relative whereas *S. doriae,* like *A. schmidti* is relatively large.

A. haasi is known only from the male holotype obtained at Dahran, eastern Saudi Arabia. In spite of being collected in 1946, no further examples have appeared, even though a great deal of *Acanthodactylus* material has been taken in the general area. *A. haasi* has much in common with *A. gongrorhynchatus* and shares a number of synapomorphies with it that occur nowhere else in the genus; these include very slender habitus, similar lateral clavula structure and reduced ear opening. It differs in its less acuminate snout and less narrowed premaxilla, shorter lateral clavula, five upper labials anterior to the centre of the eye, large and weakly keeled dorsal scales, less pectination on the fingers and numerous keels on the subdigital lamellae. In most of these features and many others *A. haasi* resembles members of the *A. cantoris* group from which *A. gongrorhynchatus* is probably derived. This together with the synapomorphies shared with the latter may indicate that *A. haasi* and *A. gongrorhynchatus* are sister species.

Another possibility, suggested partly by the fact that no further specimens have been collected, is that *A. haasi* is a hybrid between *A. gongrorhynchatus* and one of the other *Acanthodactylus* species in eastern Arabia. Assuming that a hybrid would probably be intermediate in many features, the various candidates can be considered in turn. *A. schmidti* is unlikely because its premaxilla is constricted, it has a high number of ventral scales in the longest row across the belly (13–18 compared with 10–12 in *A. gongrorhynchatus* and 12 in *A. haasi),* pectination on the fingers is extensive, multiple carination on the digits is absent (present in *A. haasi*) and, in east Arabia, it is a far larger animal than *A. gongrorhynchatus,* so interspecific copulation is unlikely; size difference would probably also exclude *A. boskianus* as well. *A. scutellatus* has a narrow premaxilla with only five teeth, dorsal scaling is fine and again there is no multiple carination on the digits. *A. opheodurus* has this feature in at least some cases and possesses all the other characteristics to be expected if *A. haasi* is a hybrid between it and *A. gongrorhynchatus.* But the status of *A. haasi* will probably only be decided by further collection in the area of the type locality.

A. schreiberi and *A. boskianus*

A. schreiberi Boulenger, 1878; Cyprus, Lebanon, N. Israel.

A. boskianus (Daudin, 1802): Much of north Africa as far south as N. Nigeria and Eritrea, Arabia but not the R'ub al Khali, S. Israel, Jordan, Iraq, Syria and adjoining Turkey.

These species are rarely found on very soft sand surfaces but occur on more stable sand and other harder substrates. *A. boskianus* is often associated with quite dense, sometimes spiny vegetation, although it also forages in more open areas (Doumergue, 1901; Flower, 1933; field labels attached to BM specimens; personal observations in southeast Arabia). Both species share a relatively high number of primitive features including the following: premaxilla with about seven teeth and not abruptly narrowed, usually 24 presacral vertebrae in males and 25 in females; fifth sternal rib often intact, hemipenis more or less symmetrical, medial side of clavula not strongly reduced; supraoculars more or less intact (first sometimes divided in *A. boskianus*), usually four upper labials anterior to centre of eye, typically 10 ventral scales in longest row across belly (12 in many Arabian *A. boskianus*), ventrals arranged in straight longitudinal rows, three longitudinal rows of scales on fingers, pectination on digits not exceptionally strong, upper caudal scales keeled, young with numerous dorsal stripes that are sometimes retained in modified form by adults. Apparently apomorphic characters include reduction of the proximal lip of the medial branch of the hemipenial sulcus, some reduction of medial side of armature, medial clavula pointed with a ⊂ -shaped cross section, lateral clavula complexly lobed, most medial of the lateral connectors broad; subocular does not usually reach mouth (exceptions in *A. boskianus*) and dorsal scales are often large. The close resemblance of *A. schreiberi* and *A. boskianus* together with the close match of their hemipenes in apomorphic features makes it very probable that they are sister species.

A. schreiberi has two allopatric populations: *A. s. schreiberi* on Cyprus and *A. schreiberi syriacus* Boettger, 1879 in Lebanon and north Israel, the latter having coarser dorsal scales with sharper keels. *A. boskianus* usually differs most obviously from *A. schreiberi* in possessing larger dorsal scales. However there is slight overlap in the transverse scale counts between the hind limbs, but not in Israel where the two species appear to contact each other without introgression (Duvdevani and Borut, 1974*b*). *A. boskianus* is the most widely distributed species of its genus but the range is not continuous in northern Africa where this lizard is mainy restricted to the periphery of the Saharan desert and to oases and other fairly mesic areas within it. As the species is relatively uniform in this region, its spread to these isolated areas may have been quite recent, presumably during one of the episodes in the Quaternary when conditions in north Africa were less extreme.

A. boskianus has been divided into three subspecies: *A. b. boskianus* in the Nile delta area and parts of Sinai; *A. b. euphraticus* Boulenger, 1919 described from Ramadieh (=Ramdi, Iraq) and *A. b. asper* (Audouin, 1829) which covers almost the whole of the species' range. This simple, tripartite division is not satisfactory, for some of the supposedly distinctive features of *A. b. euphraticus* are not consistent and there is some differentiation within the populations assigned to *A. b. asper.* An adequate intraspecific treatment of *A. boskianus* is beyond the scope of this paper but variation of some features within the species will be briefly described. Over most of north Africa, the number of dorsal scales in a transverse row at mid-body varies from about 26 to 41, although maxima are less in many areas, the first supraocular scale is usually intact and the subocular does not reach the mouth in most individuals. In the Nile delta and north Sinai, populations assigned to *A. b. boskianus* have high dorsal scale counts (34–52) and the supraocular scale is divided, but these populations intergrade with those typical of the rest of north Africa and with similar ones in Israel and west Jordan. Animals with high dorsal counts (38–48) also occur in northeast Jordan, north and central Iraq, east Syria and adjoining Turkey. In some cases, such as the types of *A. b. euphraticus,* they also have the first supraocular divided and the subocular often meeting the mouth, but these conditions are absent in many individuals from neighbouring populations. Arabian animals are rather similar to those widespread in north Africa but are characterized by low transverse dorsal scale counts at mid-body (usually 18–27 but up to 36 in the southwestern mountains) and a large body size (up to 93 mm from snout to vent against maxima of about 82 elsewhere; specimens from the western periphery of the peninsula tend to be smaller). Arabian *A. boskianus* contrast strongly with those found to the north. In Jordan an animal from the southeast of the country (El Inab, JUM R505) is of the Arabian type whereas those from elsewhere are less coarsely scaled (31–37 scales across mid-back) and relatively small (only up to about 65 mm from snout to vent). Animals of this type occur at Wadi Rum (JUM R69), only about 130 km from El Inab. Whether the two forms intergrade and, if so, whether the intergradation is abrupt is not known.

Geographical variation in *A. boskianus* may well reflect differences in niche across its range. As stated, this species is often associated with dense vegetation and large dorsal scales may well be protective where shrubs are rigid and spiny; the fine-scaled populations are in relatively mesic areas (Nile Delta, Tigris–Euphrates river system) where vegetation would be expected to be less damaging than in more arid regions. Division of the first supraocular scale and a subocular that reaches the mouth are also characters typical of more mesic situations (see p. 307). The distinctive features of lowland Arabian *A. boskianus* may be related to the fact that they coexist here with *A. opheodurus*, a small form originally confused with *A. boskianus* that occupies similar substrates and occurs in strict sympatry with it, at least in some areas (Arnold, 1980*b*). The presence of *A. opheodurus* might have produced displacement or restriction of the niche available to *A. boskianus* with consequent morphological change (Arnold, 1981*b*). Thus, increase in body size may allow adult *A. boskianus* to take larger prey, reducing competition for small food items; very large scale size could indicate that this species spends a higher proportion of time in vegetation than elsewhere. It is perhaps significant that in extreme southwest Arabia, where no *A. opheodurus* are known, *A. boskianus* is smaller with higher dorsal scale counts than elsewhere in the peninsula.

In spite of the considerable variation encountered in *A. boskianus,* as presently understood, there is as yet no firm evidence that it consists of more than one species. However, *A. schreiberi* may well have originated as an isolate of *A. boskianus.*

The *A. grandis* complex

A. grandis Boulenger, 1909 complex (including *A. fraseri* Boulenger, 1918*c*): Syria, E. Lebanon, Jordan, NW. Arabia, Iraq, SW. Iran (Khuzistan and Fars provinces—Anderson, 1974).

Nothing certain is known about the ecology of these lizards but the restricted pectination on the digits suggests that they are not usually found on very soft sand surfaces; however there is some variation in this feature between populations which may indicate that they occupy a variety of ground types. The members of the *A. grandis* complex share many features with *A. schreiberi* and *A. boskianus,* especially the former, the most significant differences being that, in the *A. grandis* complex, the ventrals are tessellated and the number in the longest row across the belly is higher (14–18), there are four longitudinal series of scales running along the fingers and the hemipenis, although generally very similar often differs slightly in the pattern of lobing on the upper surface of the lateral clavula (p. 306); also, five upper labial scales are more frequently present anterior to the centre of the eye.

Table 3 *A. grandis* complex: variation between samples

Locality	n	Maximum snout-vent length of available adults	Dorsal scales in transverse row at mid-body	Strength of keeling on dorsal scales (0–none, 4–strong)	Ventral scales in longest row across belly	Projections on free edges of sub-digital lamellae
JORDAN and SYRIA (BM, MCZ56647, including types of *A. grandis*)	6	♂103	56–64	0	16–18	several
IRAQ (localties listed from northwest to southeast)						
Hatrah, Ninevah Prov. (INHM)	2	♂70	47, 49	2	14	several
Rawa Desert (BM)	2	—	49	1	14	several
Jabal Hamrin (INHM)	1	♀62	49	4	17	several
Between Baghdad and Falluja (BM)	4	—	43–50	3	17	several
Al Uzaym, Dijla Prov. (INHM)	1	♂90	53	1	15	one
Shthath, Kerbala (INHM)	1	—	51	1	14	one
25 km S. of Najaf (INHM)	1	♂76	50	2	16	one
Nassiryah (BM)	1	♂78	49	4	16	one
Zubeya (= Az Zubayr, BM, types of *A. fraseri*)		♂73	48, 50	4	16	one
SW. IRAN (USNM 13500–01)	2	♂63	42, 44	4	14–16	one

A. grandis was originally described from the Damascus area of Syria while the only other nominal species assignable to the complex, *A. fraseri,* is based on material from Zobeya, Shariba (= Shu'aiba, northeast of Basra) far to the east in southeastern Iraq. Material collected subsequently in the intervening areas shows a variety of conditions intermediate between the named forms but the pattern of variation appears to be irregular and sometimes animals from adjacent localities show considerable differences in such features as adult size, strength of keeling on the dorsal scales, and pattern (summarized in Table 3). In general, members of the eastern populations tend to be smaller than western animals with fewer, more strongly keeled dorsal scales and single points on each subdigital lamella.

It is possible that the *A. grandis* complex is best regarded as a single species but available samples are too small and scattered to be certain about this. The irregular variation of populations intermediate between typical *A. grandis* and *A. fraseri* may reflect the geography of Mesopotamia, for here the comparatively arid country favoured by *Acanthodactylus* is divided up by the Tigris and Euphrates rivers and their tributaries which flood seasonally, so populations may be substantially discontinuous. Other *Acanthodactylus* species, especially *A. boskianus,* also show considerable variation in this area.

The *A. tristrami* group

A. (*t.*) *tristrami* (Günther, 1864): Lebanon, SW. Syria, NW. Jordan.
A. (*t.*) *orientalis* Angel, 1936: E. Syria, W. and central Iraq.
A. robustus Werner, 1929: S. Syria, SW. Iraq, Jordan and N. Arabia.

The weak digital pectination in these forms suggests that they are found on fairly hard substrates. *A.* (*t.*) *tristrami* seems to be confined to steppe-type habitats on the edge of the Anti-Lebanon range. *A.* (*t.*) *orientalis* may also be restricted to relatively mesic habitats since most records are from localities on or near the Tigris–Euphrates river system (Angel, 1936; Schmidt, 1939; Haas and Werner, 1969), although Angel also records it from Palmyra. *A. robustus,* on the other hand seems to occupy more desertic regions; Riney (1953) gives brief ecological notes that refer to this species, although they are attributed to *A.* (*t.*) *orientalis.*

Typical *A. tristrami* has many features in common with *A. schreiberi* (p. 315) but there are a number of differences: there are more presacral vertebrae, with about 25 in males and 26 or 27 in females, the proximal lip of the medial branch of the hemipenial sulcus is not reduced, the lateral clavula is complex but not lobed and is very slightly bifurcate at its tip, the first and fourth supraoculars are fragmented, the subocular reaches the mouth, the dorsal and upper caudal scales lack keels and the tail is short. Of these features, fragmentation of the supraoculars, unkeeled upper caudals, short tail, clavula shape, and perhaps vertebral number may be regarded as apomorphies. Nearly all occur in other populations of the *A. tristrami* group and unkeeled upper caudals and the short tail are confined to it.

Two other subspecies assigned to *A. tristrami* have been named, *A. t. orientalis* from eastern Syria and *A. t. iracensis,* Schmidt, 1939, described from Haditha on the Euphrates in west Iraq. The latter is said to have a lower mid-body dorsal scale count (45–46 against 48–56) and a weaker dorsal pattern than *A. t. orientalis* but other material from the same area (Haas & Werner, 1969) and from Najaf, further down the Euphrates (INHM, with 51 dorsal scales at mid-body and a bold pattern) suggest that this distinction is illusory. *A. t. iracensis* is therefore referred to the synonymy of *orientalis*. As understood here, this form is distinguished from typical *tristrami* by its smaller size (up to 63 mm from snout to vent instead of up to 92 mm) and fewer dorsal scales (43–56 against 54–65). The hemipenes are also distinctive, *orientalis* having the medial lobe and medial side of the armature very reduced. These differences suggest that *tristrami* and *orientalis* might be better regarded as full species but more information is needed before this can be confirmed.

A. robustus shares most of the distinctive features of *A.* (*t.*) *tristrami* but the lateral clavula is relatively simple, the snout is shorter and more pointed, the subocular frequently separated from the mouth, there are often 12 instead of 10 ventrals in the longest row across the belly and there may be a rudimentary fourth longitudinal row of scales on the fingers.

A. erythrurus group

A. erythrurus (Schinz, 1833): Spain, Portugal, Morocco, N. Algeria.
A. savignyi (Audouin, 1829): N. Algeria, N. Tunisia.
A. boueti Chabanaud, 1917: N. Dahomey, N. Ghana.
A. guineensis (Boulenger, 1887*a*): Ghana, Nigeria, Niger and Cameroon.

These species are typical of relatively mesic areas and usually have weak digital pectination. They are similar to *A.* (*t.*) *tristrami* in many features but all lack the short tail and unkeeled upper caudal scales of this form and also frequently have an azygos shield between the prefrontal scales.

In *A. erythrurus* and *A. savignyi* the lateral clavula of the hemipenis is deeply bifurcate at its tip, the frontonasal scale is quite often divided and the subocular may be separated from the lip.

A. erythrurus has three widespread forms: *A. e. erythrurus* in Spain and Portugal *A. e. lineomaculatus* Duméril & Bibron, 1839 in lowland western Morocco and *A. e. bellii* Gray, 1845 in the adjoining higher country and in north Algeria. Each of these is well defined on external features and *A. e. bellii* is further distinguished by its usually simple lateral clavula. Two other subspecies are sometimes recognized: *A. e. mauritanicus,* Doumergue, 1901 of extreme northern Algeria resembles *A. e. bellii* in most features including its lateral clavula and differs only in its more obviously keeled dorsals; *A. e. atlanticus* Boulenger, 1918*a* has a restricted distribution in north Morocco between the ranges of *A. e. bellii* and *A. e. lineomaculatus* and may be an intermediate between them. *A. savignyi blanci* Doumergue, 1901 of north Tunisia is very similar to *A. e. lineomaculatus* but *A. s. savignyi* which coexists with *A. erythrurus* in north Algeria is more distinctive. It has a clearly pointed snout and a better developed pectination on the digits than is usual in its close relatives which may be related to its occupying more sandy habitats (Doumergue, 1901). It is possible that the differences between the two subspecies of *A. savignyi* are a result of character displacement (Arnold, 1981*b*).

A. boueti and *A. guineensis* are generally like the above but the frontonasal is undivided and the subocular scale is never separated from the lip. Each species has a number of distinctive features. In *A. boueti* there are nine premaxillary teeth, the hemipenis is very small, the second supraocular scale is broken up and the parietal scales are partly fragmented. *A. guineensis* has the medial side of the hemipenis and armature absent and a peculiar arrangement of nasal scales (p. 296), a feature that occurs rarely also in *A. erythrurus.*

The *A. pardalis* group

A. p. pardalis (Lichtenstein, 1823): Cyrenaica, north Egypt, Israel.
A. p. bedriagai Lataste, 1881: High plateaux of north Algeria (provinces of Oran, Algiers and Constantine); closely related populations in west Morrocco and west Tunisia.
A. maculatus (Gray, 1838): northeast Morocco, north Algeria, Tunisia, Tripolitania.
A. spinicauda Doumergue, 1901: Arba Tahtani and El Abiodh Sidi Sheikh, northwest Algeria.

Members of the *A. pardalis* group are largely confined to relatively hard compact substrates such as clayey-sandy soils, clay, loess and salt flats (Blanc, 1980; Gauthier, 1967; Mosauer, 1934; data on labels attached to BM(NH) specimens).

They all agree in the following characters: premaxilla with about seven teeth, not narrowed and separated from the maxillae by a constriction. presacral vertebrae usually 24–26 in males and 25–26 in females, fifth sternal rib often interrupted; hemipenis and armature asymmetrical, often markedly so, lateral clavula often bifurcate at tip, lateral connectors often thickened; first supraocular intact or not very much divided and the fourth fragmented, subocular separated from mouth, four or five upper labials anterior to centre of eye, dorsals small and often more or less smooth, 12 or more ventrals in longest row across belly, ventrals arranged in fairly straight longitudinal rows, three longitudinal rows of scales on fingers, pectination on digits relatively weak although somewhat variable, young with numerous dorsal stripes.

Boulenger (1918*a*, 1921) treated the *A. pardalis* group as a single species within which he recognized five varieties: *pardalis* (his forma typica), *bedriagai, maculatus, latastii* Boulenger, 1918*a* and *spinicauda.* Pasteur & Bons (1960) regarded *spinicauda* as a distinct species but felt that the other varieties were no more than individual variations and placed them in the synonymy of the monotypic species *A. pardalis.* In fact, the introduction of osteological and hemipenial data helps to confirm the validity of the majority of Boulenger's divisions and it appears that at least five entities within the *A. pardalis* group can be recognized (see Table 4 & Fig. 7), *A. maculatus,* as understood here, includes Boulenger's var. *latastii.* This author restricted *maculatus* to often relatively small-bodied populations in which the posterior dorsal scales are frequently keeled and some individuals have light stripes or rows of light spots. These are distributed along the coastal areas of Tripolitania and

Table 4 Variation within the *Acanthodactylus pardalis* group

	A. p. pardalis	*A. p. bedriagai*	Un-named west Moroccan population	*A. maculatus*	*A. spinicauda*
Hemipenis lacks medial lobe and medial section of armature	–	–*	–	+	+
Usual number of presacral vertebrae: males	24/25	26	26	24	24
females	25(26)	26	26	25	26
Approximate number of animals in which 5th sternal rib is interrupted	20/24	7/14	4/9	48/62	7/10
Number of ventral scales in longest transverse row	12(14)	14(12, 16)	12	12(14)	12
Longitudinal rows of ventral scales	27–34	31–36	30–34	27–33	27–33
Keeling on dorsal scales often quite strong	–	–	+	+/–	+
Enlarged, tubercular scales on sides of tail base	–	–	–	–	+

*excluding population from Tamesmida, see below.

Tunisia and in northeast Algeria. The name *latastii* was applied to inland populations lying mainly to the south in which body size is sometimes greater, dorsal scales are usually more or less smooth, the dorsal pattern tends to lack light stripes or spots and the snout is more pointed. However, there is considerable variation and many intermediates occur, so it seems best to regard these populations as a single unit. The geographical differences within this may reflect change in vegetation and substrate conditions; the pattern of *maculatus*-type animals is more likely to be cryptic where vegetation is relatively dense whilst that typical of *latastii* is probably cryptic in more open areas.

The relationships between the forms described in Table 4 are not entirely clear, but it is certain that they cannot all be assigned to a single species. Although no areas of certain sympatry are known, *bedriagai,* the form of the high plateaux of north Algeria, approaches the more southern *maculatus* near Biskra (*bedriagai*—Aures Mountains north of Biskra, BM(NH) 91.5.4.70–72; *maculatus*—near Biskra, BM(NH) 1907.4.6.10–25, BM(NH) 1920.1.20.791, BM(NH) 1969.2121–23). The two localities are probably within 100 km of each other but the forms retain their differences in hemipenial structure, usual number of presacral vertebrae and of ventral scales in the longest row across the belly, and in pattern. It seems likely therefore that *bedriagai* and *maculatus* are distinct species, especially as the hemipenial differences between them could act as an isolating mechanism.

The un-named west Moroccan population (north of Agadir, BM(NH) 1970.246–47; 20 km north of Tiznit, BM 1970.248; 30 km southwest of Goulmime, BM(NH) 1970.249–50) is generally similar to *bedriagai* and is probably conspecific with it but differs in the following features: snout often more pointed, posterior dorsal scales more pointed and keeled, ventrals in longest row across belly often 12 (not 14), upper labials anterior to centre of eye often four (frequently five in *bedriagai*), range of dorsal patterns somewhat different. It is possible that this population also contacts *A. maculatus* although evidence is lacking.

Another *A. bedriagai*-like population occurs at Tamesmida (33.05N 8.23E) in western Tunisia (BM(NH) 1920.1.20.3018, discussed by Boulenger, 1921, p. 67). The two male specimens available resemble this form very closely in osteological features and externals but the hemipenis is single-lobed and the median side of the armature is lacking. Close by at

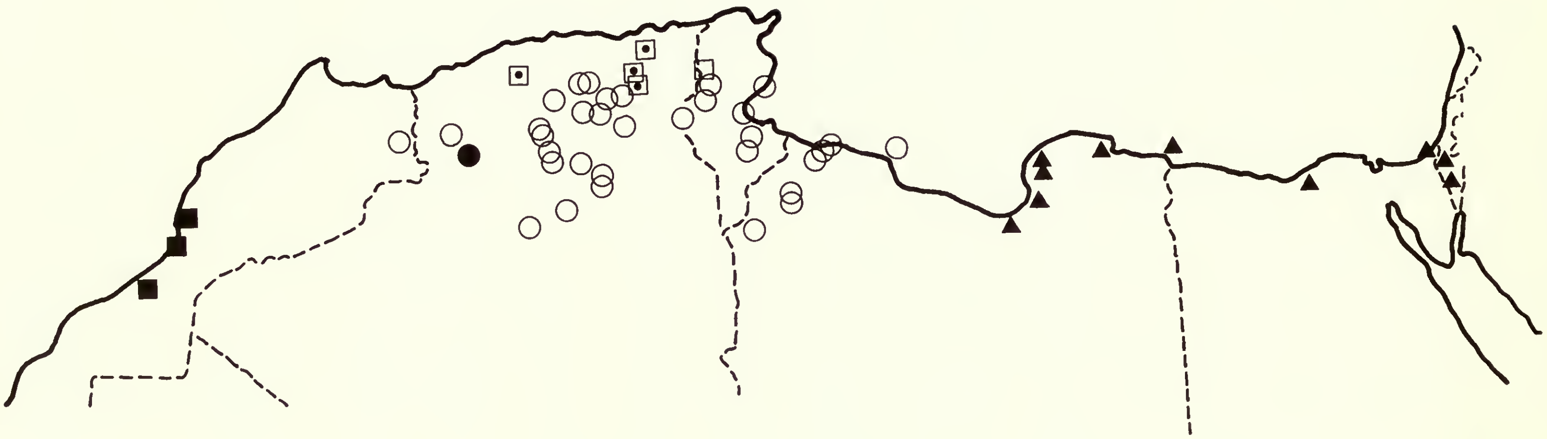

Fig. 7 Distribution of the *A. pardalis* group based largely on material in the British Museum (Natural History). ▲–*A. p. pardalis*; ⊡–*A. p. bedriagai*; □–*A. p. bedriagi*-like population from near Tamesmida (see p. 000); ■–un-named West Moroccan population similar to *A. p. bedriagai*; ○–*A. maculatus*, ●–*A. spinicauda*.

Furryanah (34.57N 8.35E), *A. maculatus* occurs (BM(NH) 1920.1.20.3018e) but, as the Tamesmida specimens are not like this form in other respects, a hybrid origin for them seems unlikely. Possibly they represent an isolate of the *A. bedriagai* stock that has undergone hemipenial modification in response to some previous threat of introgression, as seems to have happened several times in *Acanthodactylus* (p. 304). Tamesmida is on the edge of the eastern extension of the high ground on which *A. bedriagai* is found.

The form *spinicauda* is known only from Arba Tahtani (=Arbaouat, 33.05N 00.35E) and nearby El Abior Sidi Sheikh (=El Abiodh Sidi Cheikh, 32.53N 00.34E), oases at the southern foot of the Saharan Atlas in northwest Algeria. In general form, hemipenial structure and pattern, it resembles *A. maculatus* populations in the region (Mecheria and Laghouat) but differs in having the lateral scales at the base of the tail greatly enlarged, especially in males, with their keels produced to form tubercles, this condition occurring in no other lacertid. The hind legs are also rather longer than in nearby *A. maculatus* populations, although this is partly due to the fact that relative hind-leg length decreases with size and *spinicauda* is quite small; three females radiographed all have 26 presacral vertebrae instead of the 25 usual in *A. maculatus*. The two forms do not appear to be sympatric, so a direct test of the species status of *spinicauda* is not possible. It is certainly very like neighbouring *A. maculatus* but the three distinctive features, especially the unique tail structure, suggest it may be best to regard it as a full species, at least for the present. In the south of its range, *maculatus* appears to have a disjunct distribution, occurring mainly around oases such as Ouargla, Ghardia and Leghouat. Presumably its range was once more continuous but has become fragmented since the climate of the area has become more extreme. It is probable that *A. spinicauda* originated from such an oasis isolate.

Typical *A. pardalis* show some variation, for instance animals from the Jebel el Akhdar region of Cyrenaica appear to be smaller than samples to the south and east. Also, although Egyptian animals usually have 24 presacral vertebrae in males and 25 in females, in Cyrenaica 25 is common in males and females sometimes have 26. While there is evidence that *bedriagai* and *maculatus* are specifically distinct, it is less clear how they are related to typical *A. pardalis*. This is partly because neither is known to contact this form, there being a gap in the known range of the *A. pardalis* group as a whole south of the Gulf of Sirte, Libya, although whether this is real or a collecting artifact is uncertain. Typical *A. pardalis* resembles *bedriagai* in hemipenial structure but differs in usual number of presacral vertebrae and ventral scales in the longest row across the belly (although the *bedriagai*-like population in west Morocco matches *pardalis* in this last characteristic). On the other hand, *A. pardalis* resembles *maculatus* in these features and the nearest populations of each form are quite similar, although coastal *maculatus* west of the Gulf of Sirte are smaller and have more strongly keeled dorsal scales than the closest *pardalis*. However, these two forms differ radically in hemipenial structure which, coupled with size-difference in this area might well preclude interbreeding. This being so, it seems reasonable to regard *maculatus* as specifically distinct from *pardalis*, although it cannot be ruled out that connecting populations may yet be found in north Libya with intermediate hemipenes. Typical *bedriagai* and the similar west Moroccan population are tentatively regarded as conspecific with *pardalis* as they are hemipenially similar and the differences between them are mainly in features showing substantial variation within each population. On hemipenial evidence, the Tamesmida population may be specifically distinct from *A. bedriagai* but it seems safest to leave its status undecided until more is known about it.

The *A. scutellatus* group

A. scutellatus (Audouin, 1829): North Africa south to Senegal, Mauretania, Mali, Niger, N. Chad and N. Sudan; S. Israel, N. Arabia, S. and central Iraq.

A. longipes Boulenger, 1918*a*: North Africa including parts of S. Morocco, Algeria, Libya, Mauretania, Mali, Niger and Chad.

A. aureus Günther, 1903; Coasatal areas of NW. Africa from S. Morocco to Mauretania; also some neighbouring inland areas.

The *A. scutellatus* group is largely associated with soft-sand habitats (Anderson, 1898; Doumergue, 1901; Flower, 1933; Mosauer, 1934; Gauthier, 1967; Blanc, 1980; field labels on BM(NH) material); this is also suggested by the extensive pectination usually present on the toes. However occasional populations are found on harder substrates (Scortecci, 1946). In north Africa the group occupies many desert areas and, unlike *A. boskianus* in this region, is not largely confined to relatively mesic enclaves. *A. scutellatus* and its relatives have few features plesiomorphic within *Acanthodactylus* but many apomorphic ones including the following: premaxilla often with only five teeth and abruptly narrowed, usual number of presacral vertebrae 23 or 24 with very little sexual variation, fifth sternal rib interrupted in a high proportion of individuals; medial lobe of hemipenis, medial branch of sulcus and medial side of armature absent or greatly reduced, clavula with a ⊃-shaped cross section; subocular scale separated from mouth, five or six upper labial scales anterior to centre of eye (four in *A. aureus*), (10)12–18 ventral scales in longest row across belly; ventrals tessellated, four longitudinal rows of scales on fingers, pectination on digits usually strong; young often uniform above.

The populations that constitute the *A. scutellatus* group show great variation in some features: maximum adult size ranges from about 50 mm from snout to vent to nearly 80 mm, dorsal scales may be coarse and keeled or fine and smooth, transverse counts at mid-body ranging from 36 to 100, number and degree of tessellation of ventral scales varies as does amount of pectination on digits and dorsal pattern ranges from stripes or rows of spots to reticulation or uniformity. From analogy with other species in the genus, keeled dorsal scales, low scale counts, reduced ventral tessellation, limited pectination and striped patterns are all likely to be associated with habitats that have harder substrates and more extensive vegetation, whereas contrasting conditions may be typical of soft, open sand.

Although the *A. scutellatus* group is easily defined, recognition of taxa within it is difficult. Boulenger, (1918*a*, 1921) treated it as a single species with six varieties. Bons & Girot (1962) pointed out that, as some of these were sympatric, they could not be regarded as mere subspecies and suggested the following arrangement for Boulenger's taxa; they also included a form named by Haas (1957) and another described by themselves.

A. scutellatus scutellatus (Audouin, 1829): Egypt, Israel, Sudan.
A. scutellatus hardyi Haas, 1957: Arabia, S. Iraq.
A. scutellatus audouini Boulenger, 1918*a*: S. Egypt, Libya, S. Tunisia, S. Algeria.
A. longipes longipes Boulenger, 1918*a*: S. Libya, Algerian Sahara.
A. longipes panousei Bons & Girot, 1962: SE. Morocco.
A. inornatus inornatus (Gray, 1838): N. Libya, Tunisia, N. Algeria, S. Morocco.
A. inornatus aureus Günther, 1903: Atlantic coast from S. Morocco to Port Etienne.
A. dumerilii (Milne-Edwardes, 1829): Senegal, Mauretania, Niger.

But this system too presents problems for there is no real evidence that *A. scutellatus, A. inornatus* and *A. dumerilii* act as good species, nor is it clear that *A. i. inornatus* and *A. i. aureus* are conspecific. Difficulties in the interpretation of the *A. scutellatus* group arise partly because intrapopulational variation is great and there are large areas in its huge range where material is unavailable. Problems also stem from the geographical structure of the group. The soft-sand habitats favoured by these lizards are by no means continuous and consist of a series of isolates and semi-isolates which have almost certainly had a complicated history of contraction and expansion, and contact and isolation (see, for instance Sarnthein, 1978). The lizard populations associated with these different, partly discrete habitat units are likely to have been subjected to differing selective regimes and even neighbouring populations may show differences. However, although the *A. scutellatus* group exhibits great variation, it is mainly in a few characters that are likely to be ecologically correlated and it seems possible that similar morphotypes may have developed independently in some cases.

Sometimes, populations may have evolved differences while isolated that enable them to act as good species if contact is restored. Such areas of sympatry or parapatry would provide the best evidence of speciation within the *A. scutellatus* group but, in the stringent environments inhabited by these lizards, the niche space they usually occupy may often be able to support only one species, so that areas of extensive sympatry may be uncommon and regions of contact will frequently be very restricted. Given the poor sampling available, places where two species occur together will not be very easy to find. Nevertheless they do exist and there are others where quite different populations approach each other very closely. On the basis of such localities, the *A. scutellatus* group is best divided into three species *A. scutellatus, A. longpipes* and *A. aureus.*

A. scutellatus

As understood here, this widespread species consists of populations in which there are typically less than 70 dorsal scales in a transverse row at mid-body and not usually more than 14 ventral scales in the longest row across the belly (exceptions to both frequent in Egypt and neighbouring areas), five or six upper labial scales anterior to the centre of the eye, premaxilla typically with five teeth, most usually 24 presacral vertebrae and dorsal coloration highly variable. Variation is summarized in Table 5. The name *A. scutellatus* was originally applied to the often large, frequently reticulated, fine scaled populations of northern Egypt. The var. *audouini* of Boulenger is said to differ in usually having spots or vermiculations and in its coarser, keeled dorsal scales but individuals assignable to these two forms occur in the region of Wadi Halfa, Sudan, alongside intermediates and animals from Kufra cannot be convincingly assigned to one form or the other. Other examples attributed by Boulenger to var. *audouini* occur on the coast of Tripolitania but extensive material now in the British Museum (Natural History) shows that these intergrade with other samples assignable to the small var. *inornatus.* The snout-length difference between these forms mentioned by Boulenger is very difficult to demonstrate and is complicated by allometric changes. It seems very improbable, on present evidence, that two species are represented by these samples.

Animals from Mauretania and Senegal were assigned by Boulenger to var. *dumerilii,* regarded as a full species by Bons and Girot. This form is characterized by usually small size, coarse dorsal scales, low ventral number and sometimes striped dorsal patterns. But, if samples are compared, there is a gradual change from south to north the numbers of dorsals and ventrals increasing and striping disappearing (Table 5, localities N–J). The most northern animals are extremely similar to the next available samples in northern Algeria and there are certainly no differences that would suggest they are not conspecific.

In summary, the forms *scutellatus, audouini, inornatus* and *dumerilii* are not discrete and, on present evidence, cannot be separated at the species level. The pattern of geographical variation in *A. scutellatus* seems too complex to assign subspecies names in any consistent way, at least at present.

A. longipes

This species can be distinguished from sympatric or parapatric *A. scutellatus* by its higher mid-dorsal transverse scale count (usually over 70 and always over 65), typically greater number of ventral scales in the longest row across the belly (often more than 14) and frequently lower presacral vertebral count (usually 23); the dorsum is typically very pale, either plain or with a reticulation on the flanks. These differences, together with its usually greater pectination on the toes, suggest that it occupies softer, more open sand than *A. scutellatus,* where they occur together. A number of contact or approach areas are known. In northern Algeria, there may be considerable geographical overlap but in Mauretania only a narrow abutment seems to be present with *A. scutellatus* in the west and *A. longipes* in the

Table 5 *Acanthodactylus scutellatus*: geographical variation. Locality letters refer to Fig. 8.

	n	Dorsal scales in transverse row at mid-body	Ventral scales in longest row across belly				Known maximum length, snout to vent (mm)	Strength of keeling on dorsal scales (0–none, 4–strong)	Usual dorsal pattern (r–reticulation, p–plain v–vermiculation, s–spots, st–longitudinal streaks)
			10	12	14	16			
A. Arabia	51	46–61		12	21	1	61	0	r,v
B. North Egypt	33	64–80		1	30	2	72	0,1	r(occasionally v or s)
C. Jalo, Libya	2	65–70			2		67	3	v
D. North Cyrenaica	13	50–61		2	8		61	2	often r
E. Inland West Libya	20	55–66			19	1	60	2	r,v
F. Coastal Tripoli, Tunisia	64	50–62		8	10		72	4	♂♂ often v or s or weak r ♀♀ p or s
G. North Algeria	68	40–65		4	64	4	62	4	♂♂ s or weak r, ♀♀ p or s
H. Central Algeria	3	66–67			2	1	77	4	v or p
J. Fort Gouraud	18	56–66		12	6		52	4	♂♂ r or s, ♀♀ s in lines
K. Atar	56	43–58	1	12	3		56	4	s
L. Akjoujt	12	44–57		10	2		54	4	s or st
M. Nouakchott	23	40–52		17	2		50	4	s, r or st
N. Senegal	20	36–47		20			55	4	r or st
P. Mali, Niger, NW Chad	11	51–63			11		64	2	v or s
Q. Kufra	10	60–73			7	1	72	3	♂♂ v, ♀♀ s
R. SW Egypt, Sudan	24	54–73		1	13		72	3,4	r, v or s

Table 6 *Acanthodactylus longipes*: geographical variation. Locality numbers refer to Fig. 8.

		A. longipes						Nearest *A. scutellatus* populations					
	n	Dorsal scales in transverse row at mid-body	Ventral scales in longest row across belly			Femoral pores	Known maximum length from snout to vent (mm)		Dorsal scales in transverse row at mid-body	Ventral scales in longest row across belly			Known maximum length from snout to vent (mm)
			14	16	18					12	14	16	
N. ALGERIA, MOROCCO													
1. Tuggurt	1	65		1		22–23	60	Tuggurt	51–62	1	3		55
2. Ouargla	4	75–80		4		24–29	62	Ouargla	49–57		6		52
3. Kerzaz	3	81–86		2	1	19–23	59	Ain Sefra	48–65		10	2	55
4. Erg Chebbi, Morocco (Bons & Girot, 1962)	4	73–80	1	3		18–23	53	Ain Sefra	48–65		10	2	55
MAURETANIA, N. MALI													
5. Chinguetti	4	70–80	1	2	1	20–24	53	Chinguetti	43–58	3	1		56
6–10. Other localities	8	77–97	1	4	1	23–27	61	Chinguetti, E. Mali	51–63		7		64
11. NIGER	1	77		1		22		20N 8.40E	53		1		59
SW. LIBYA													
12, 13. Zouarke, Merzouk	3	69–80	2			23–25	55	Merzouk	55		1		
'Race B' (Scortecci, 1946)		72–92	+	+		18–26	56	'Race A'	50–78	(+)	+		63
14. N. CHAD	3	70–82	2	1		19–21	55	Zouarke	62	1			48

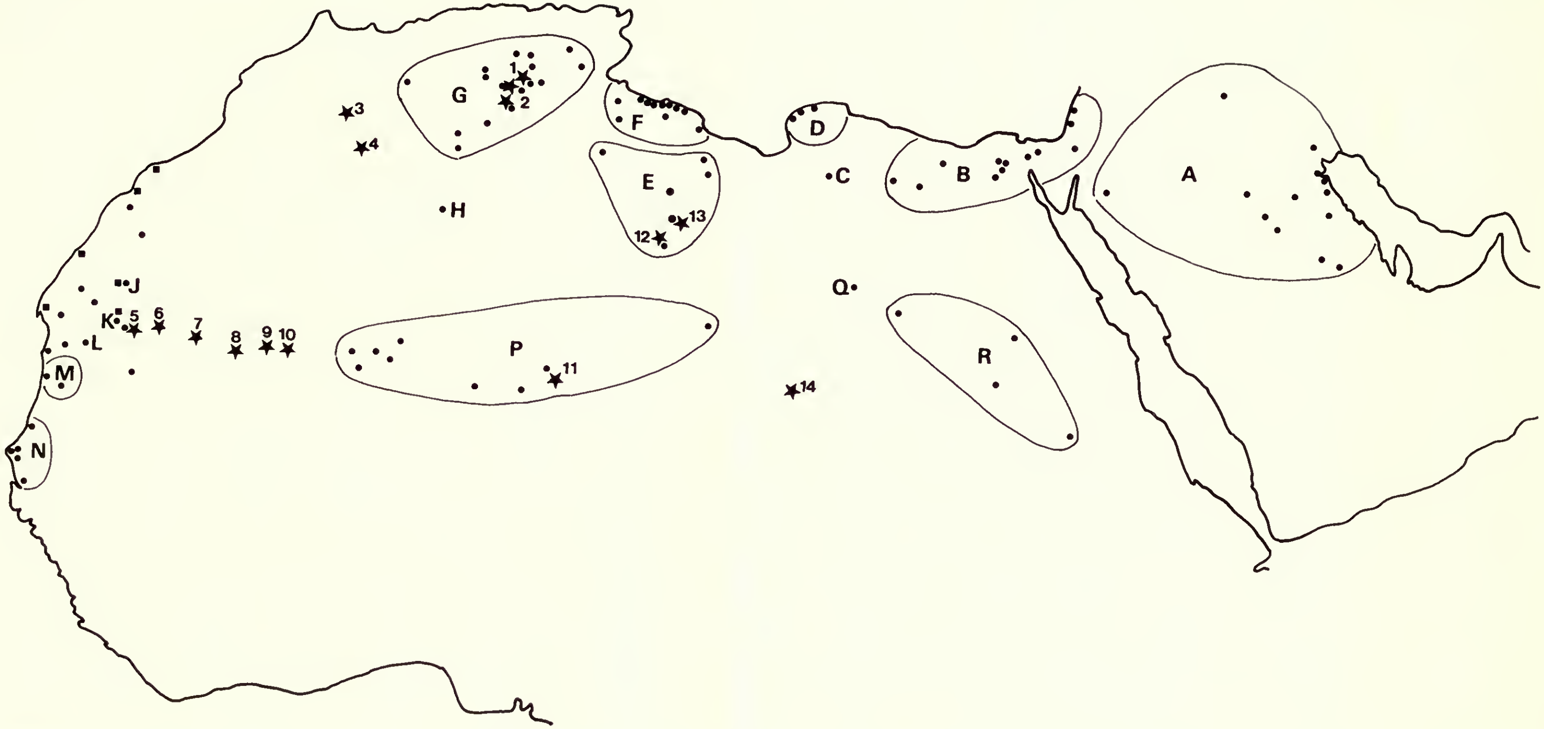
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Fig. 8 Distribution of the *A. scutellatus* group based largely on material in the British Museum. ●–*A. scutellatus*; ★–*A. longipes*; ■–*A. aureus*. Letters, for groups of *A. scutellatus* localities defined by thin lines, and figures for individual *A. longipes* localities refer to Tables 5 and 6.

east. In south Libya sympatry may be quite extensive, as indicated by Scortecci, 1946 (his group A is apparently *A. scutellatus* and group B is *A. longipes*). This author's observations give some support to the ecological separation between the two species suggested above.

Localities for *A. longipes* are very scattered and, given the disjunct nature of the sort of habitat that it occupies, this species may consist of several quite isolated populations.

A. aureus

The populations found along the Atlantic coast of northwest Africa are all rather similar and in many respects resemble neighbouring *A. scutellatus* (referred by Bons and Girot to *A. i. inornatus*). They differ most obviously from this species in having only four upper labial scales anterior to the centre of the eye, seven teeth in the premaxilla and the snout is often more acuminate. Such animals, typical of *A. aureus*, may occur some way from the coast (e.g. at Uedi Taamia, 26.01N 13.12W; EBD 2450) but at present they are not known to contact *A. scutellatus*. However, at two localities in Mauretania, the latter occurs alongside another form that may well be conspecific with *A. aureus*. If so this provides some evidence that the latter is a good species. The animals concerned are from Fort Gouraud (♂♂, BM(NH) 1982.292–93) and Atar (♀, BM(NH) 1982.294) and are compared with sympatric *A. scutellatus* in Table 7. They are very similar to typical *A. aureus* in most features and it seems likely that they are referrable to this species.

The inter-relationships of the three species that make up the *A. scutellatus* group are unclear. A priori, *A. aureus* might be considered the most primitive, often having seven premaxillary teeth and four upper labials anterior to the centre of the eye. But, if the Mauretanian specimens with five premaxillary teeth are assignable to *A. aureus*, this apomorphic feature cannot be used to unite *A. scutellatus* and *A. longipes* as sister species. Also, the presence of four, instead of five or six upper labials, may be secondary, for other species with acuminate snouts (*A. gongrorhynchatus*, *A. masirae*) have lower labial scale counts than expected from their phylogenetic relationships judged by other features.

Table 7 *A. aureus*: comparison of samples with neighbouring *A. scutellatus*

	Fort Gouraud, Atar *scutellatus*	 *aureus*	Coastal area *aureus*
Upper labial scales anterior to centre of eye	5 or 6	4	4
Dorsal scales across mid-body	45–56	38–46	41–60
Lower temporal scales	large, often keeled	large, smooth	usually small, smooth
Enlarged gular scales bordering 4th and 5th chin shields	frequent	none	rare
Usual number of rows of granules beneath centre of collar	2 or 3	0	0 or 1
Usual number of premaxillary teeth	5	5	7
Pattern of males	Fine spots or reticulation	coarse spots	coarse spots or vermiculation

The *A. opheodurus* group

A. opheodurus Arnold, 1980*b*: Arabia (but not apparently the southern desert or northern Oman), S. Israel, Jordan, parts of Iraq.
A. felicis Arnold, 1980*b*: S. Arabia (Republic of South Yemen and Dhofar, S. Oman)
A. masirae Arnold, 1980*b*: S. Oman.

This assemblage consists of three small species, all wholly or largely confined to Arabia. All have only recently been described for, although *A. opheodurus* and *A. felicis* have been present in museum collections for some time, they have been confused with *A. boskianus*. These lizards appear to be associated with relatively hard substrates and have restricted pectination on the digits.

The group possesses a high proportion of plesiomorphic features: premaxilla with about seven teeth and not abruptly narrowed (except in *A. masirae*), usually 24 presacral vertebrae in males and 25 in females, fifth sternal rib usually intact; lateral clavula simple, hemipenial connectors unthickened; first supraocular more or less intact, typically four upper labial scales anterior to the centre of the eye, eight or ten ventral scales in longest row across belly, ventrals arranged in straight longitudinal rows, three longitudinal rows of scales around fingers (a fourth row in *A. masirae*), pectination on digits not strong, upper caudal scales keeled, young striped dorsally, the stripes sometimes persisting in adults. However the hemipenis is highly modified in the *A. opheodurus* group, the medial lobe and medial side of the armature being greatly reduced, the fourth supraocular scale is at least partly broken up and the subocular scale is often separated from the mouth (not in *A. masirae*) and the number of stripes in the juvenile pattern shows some reduction. Dorsal scaling is relatively coarse, there being 25–42 scales in a transverse row across the mid-body.

The three species are grouped together largely on the grounds of overall similarity.

Inter-relationship of the species of *Acanthodactylus*

The approach used for estimating the phylogeny of the species of *Acanthodactylus* is briefly discussed on p. 293. Probably derived character states shared by two or more species (provisional synapomorphies) are listed in Table 8 and their distribution shown in Table 9. Polarity, that is which state of a character is primitive and which state or states derived, has been decided largely by outgroup comparison, using the rest of the Lacertidae as the outgroup. Some assessment of the relative reliability of characters as indicators of relationship (character weighting) was attempted employing the indicators mentioned by Arnold (1981*a*). No features scored very well on this basis and most scored quite badly but among the better ones were the following (numbers refer to Tables 8 & 9, and Fig. 9): premaxillary teeth reduced to five (1); hemipenial features not thought to be connected directly with the development of physical isolating mechanisms against interbreeding discussed on p. 304 (9, 11–17); reduction in size of the ear opening (24); no keeling on proximal dorsal caudal scales (30). These features are consequently given some precedence in situations where the evidence of different derived character states conflicts. Because many features are polymorphic, with both the primitive and a derived state occurring together in the same species, Le Quesne's (1969) method for determining compatible characters could not be used. As well as joint possession of derived character states, strong overall resemblance is also taken as prima facie evidence of close relationship. Using these indicators, a provisional partial phylogeny of *Acanthodactylus* was constructed and is shown in Fig. 9.

The relationships of the *A. cantoris* group, *A. gongrorhynchatus* and *A. haasi* are discussed on p. 311. By and large, the hypothesis of their relationships shown in Fig. 9 involves a pattern of shared apomorphies that does not include much homoplasy. As stated, the main conflict involves the position of *A. schmidti*: is it more closely related to *A. arabicus* or to *A. blanfordii*? The former relationship is supported by total loss of the medial side of the hemipenis and armature (8d, 10c) and some increase in the number of ventral scales (26b),

Table 8 Probable derived character states shared by two or more species of *Acanthodactylus*. Where features appear to constitute a transformation series, they are listed in their supposed order of origin and denoted by a consecutive letter thus: a, b, c, d.

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1. Premaxilla narrowed: a. somewhat; b. distinctly.
2. Premaxillary teeth reduced to five.
3. Presacral vertebrae 23 or 24 in females.
4. Presacral vertebrae 26 or 27 in females.
5. On average, females have less than one more presacral vertebra than males: a. 0·66–0·84 more vertebrae; b. 0·07–0·33 more vertebrae.
6. Fifth sternal rib interrupted in over 50% of individuals.
7. Hemipenis small.
8. Medial lobe of hemipenis reduced: a. somewhat reduced; b. more strongly reduced; c. very small; d. minute or absent.
9. Proximal lip of medial branch of hemipenial sulcus reduced to a fold in symmetrical hemipenes.
10. Medial side of armature reduced: a. somewhat reduced; b. more strongly reduced; c. reduced to a thread or absent.
11. Medial clavula narrow and pointed with a ≺-shaped cross section.
12. Lateral clavula with a proximally directed pocket.
13. Lateral clavula very narrow.
14. Lateral clavula complexly structured with multiple lobes below.
15. Lateral clavula complexly structured and divided at tip.
16. Lateral clavula folded with ⊃-shaped cross section.
17. Most medial connector on lateral side of hemipenis thickened.
18. Nostril separated from first upper labial scale by a subnasal.
19. Frontonasal scale longitudinally divided.
20. One or two azygos scales present between the prefrontal scales.
21. Supraocular scales not all intact: a. an area of granules wedged between the third and fourth supraoculars and the latter sometimes divided; b. first supraocular divided into two or three, fourth supraocular very fragmented; c. first and fourth supraoculars very fragmented; d. first, second and fourth supraoculars very fragmented.
22. Subocular scale usually separated from mouth.
23. Upper labial scales anterior to centre of eye more than four.
24. Ear opening reduced in size.
25. Dorsolateral tracts of enlarged scales on posterior body.
26. Maximum number of ventral scales in a transverse row: a. 12; b. 14 or more.
27. Ventral scales tessellated: a. at sides only; b. generally.
28. Ventral scales grade into dorsals: a. to a small extent; b. more generally.
29. Four longitudinal rows of scales on the fingers: a. anterior row irregular; b. anterior row regular and continuous.
30. No keeling on proximal dorsal caudal scales.
31. Tail less than 1·5 times snout-vent distance.
32. Occipital stripes fuse to form a mid-dorsal band (often not visible in adults): a. fusion does not extend to occiput; b. fusion extends to occiput.
33. Young without pattern of light and dark stripes.
34. Reddish-brown spots present in pattern that do not fade in alcohol.
35. Two rows of large ocellar markings along back.

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while affinity to *A. blanfordii* is suggested by similarity in lateral clavula structure (12) and the presence of dorsolateral tracts of enlarged scales (25). The former characters appear weaker indicators of relationship, especially as they have developed several times in the Lacertidae, while characters 12 and 25 are known nowhere else. *A. schmidti* is consequently regarded as the sister species of *A. blanfordii*. Whether *A. haasi* is the sister species of *A. gongrorhynchatus*, which is suggested by its slender habitus, reduced ear opening (24) and some features of the lateral clavula (p. 306), or a hybrid between this species and another such as *A. opheodurus*, is discussed elsewhere (p. 314).

Table 9 Distribution of probable derived features among the species of *Acanthodactylus*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
A. micropholis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. cantoris	—,a	—	—	—	—	—	a	—	—	—,a	—	—	—	—	—	—	—	—	—,(a)
A. blanfordii	b	—	—,(a)	—	a	—	—	a	—	b	—	a	—	—	—	—	—	—	—
A. schmidti	b	—	—,a	—	—,b	—	—	d		b,c	—	—,(a)	—	—	—	—	—	—	—
A. arabicus	b	—	—,(a)	—	—	—	—	d		c		—	a	—	—	—	—	—	—
A. gongrorhynchatus	b	—	—,a	—	—	—	—	d		c		—	a	—	—	—	—	—	—
A. haasi	b	—	—	—	—	—	—	d		c		—	a?	—	—	—	—	—	—
A. schreiberi	—	—	—	—,a	—	—	—	—	a	a	a	—	—	a	—	—	a	—	—
A. boskianus	—,a	—	—,a	—,(a)	a	—	—	—	a	a	a	—	—	a	—	—	a	—	—,(a)
A. grandis	—	—	—	—	—	—	—	—	a	a	a	—	—	a	—	—	(—),a	—	—
A. (t.) tristrami	—	—	—	a	—	—	—	—	—	a	a	—	—	—	—	—	a	—	—
A. (t.) orientalis	—	—	—	a	—	—	—	c	—	b	—	—	—	—	a	—	a	—	—
A. robustus	—	—	—	a	—		—	—	—	a	a	—	—	—	—	—	a	—	—
A. erythrurus	—	—	—	(—),a	—	—	—	—	—	a	a	—	—	—	a	—	a	—,(a)	—,a
A. savignyi	—	—	—	a	—	—	—	—	—	a	a	—	—	—	a	—	a	—	—,a
A. boueti	—	—	—	a	—	—	a	—	—	a	a	—	—	—	a	—	a	—	—
A. guineensis	—	—	—	a	—	—	—	d		c		—	—	—	—	—	a	a	—,(a)
A. pardalis pardalis	—	—	—	—,(a)	a	a	—	b	—	a	a	—	—	—	a	—	a	—	—
A. pardalis bedriagae	—	—	—	a	b	a	—	b	—	a	a	—	—	—	a	—	a	—	—
A. maculatus	—	—	—,(a)	—,(a)	—	a	a	d		c		—	—	—	—,a	a	a	—	—
A. spinicauda	—	—	—	—	—	a	a	d		c		—	—	—	—	a	a	—	—
A. aureus	b	—,a	(—),a	—	b	a	—	d		c		—	—	—	—	a	—	—	—
A. scutellatus	b	a	(—),a	—	b	a	—	d		c		—	—	—	—	a	—	—	—,(a)
A. longipes	b	a	a	—	b	a	—	d		c		—	—	—	—	a	—	—	—
A. opheodurus	—,a	—	—,(a)	—,(a)	a	—	—	d		c		—	—	—	—	—	—	—	—
A. felicis	—	—	—	—	a	—	—	d		c		—	—	—	—	—	—	—	—
A. masirae	b	—	—	—	—	—	—	d		c		—	—	—	—	—	—	—	—

Table 9 continued

	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
A. micropholis	–	b	–,(a)	(–),a	–	–	–	–	–	–,(a)	–	–	–	–	–	–
A. cantoris	–,(a)	a	a	(–),a	–	–	a,(b)	–,a	–	(a),b	–	–	–	–	–	–
A. blanfordii	–	a	a	a	–	–,(a)	a,(b)	a	–	b	–	–	–	–	–	–
A. schmidti	–	a	a	a	–	b	b	a	–	b	–	–		a	–	–
A. arabicus	–	a	a	a	–	–	(a),b	a	a	b	–	–	–	–	–	–
A. gongrorhynchatus	–	a	a	–	a	–	a	a	b	b	–	–	–	–	–	–
A. haasi	–	a	a	a	a	–	a	–	b	b	–	–	–	–	–	–
A. schreiberi	–,(a)	–	a	–,(a)	–	–	–	–	–	–	–	–	–,(a)	–	–	–
A. boskianus	–,(a)	–,a	(–),a	–,(a)	–	–	–,(a)	–	–	–	–	–	–,(a),(b)	–	–	–
A. grandis	–,(a)	–	a	–,(a)	–	–	b	b	–	b	–	–	–	–	–	–
A. (t.) tristrami	–	c	–	–	–	–	–	–	–	–	a	a	–	?	–	a
A. (t.) orientalis	–	c	–	–	–	–	–	–	–	–	a	a	–	?	–	a
A. robustus	–	c	a	–	–	–	(–),a	–	–	a	a	a	–	?	–	a
A. erythrurus	–,a	c	–,a	–,(a)	–	–	–	–	–	–	–	–	–	–	–	–
A. savignyi	(–),a	c	–,a	–	–	–	–,(a)	–	–	–	–	–	–	–	–	–
A. boueti	a	d	–	–,(a)	–	–	–	–	–	–	–	–	–	–	–	–
A. guineensis	–,(a)	c	–	–	–	–	–	–	–	–	–	–	–	–	–	–
A. pardalis pardalis	–	b	(–).a	(–),a	–	–	a,(b)	–	–	–	–	–	–,(a)	–	–,a	–
A. pardalis bedriagae	–	b	(–),a	(–),a	–	–	a,b	–	–	–	–	–	–	–	–	–
A. maculatus	–	b	(–),a	–,a	–	–	a,(b)	–	–	–	–	–	–	–	–,a	–
A. spinicauda	–	b	(–),a	–	–	–	a	–	–	–	–	–	–	–	–	–
A. aureus	–	a	a	–,(a)	–	–	(a),b	b	–	b	–	–	–	–	–	–
A. scutellatus	–	a	a	(–),a	–	–	(–),a,b	a,b	–	b	–	–	–,(a),(b)	–,a	–	–
A. longipes	–	a	a	a	–	–	b	b	–	b	–	–		a	–	–
A. opheodurus	–	a	(–),a	–,(a)	–	–	–,(a)	–	–	–,(a)	–	–	(a),b	–	–	–
A. felicis	–	a	a	–	–	–	–	–	–	–	–	–	–,(a)	–	–	–
A. masirae	–	a	–	–	–	–	–	–	–	a,b	–	–	–,(a)	–	–	–

– indicates primitive states; a indicates derived features; a, b, c . . . indicate successive states in a transformation series; no entry indicates that the character cannot be scored; brackets indicate that the state concerned is uncommon.

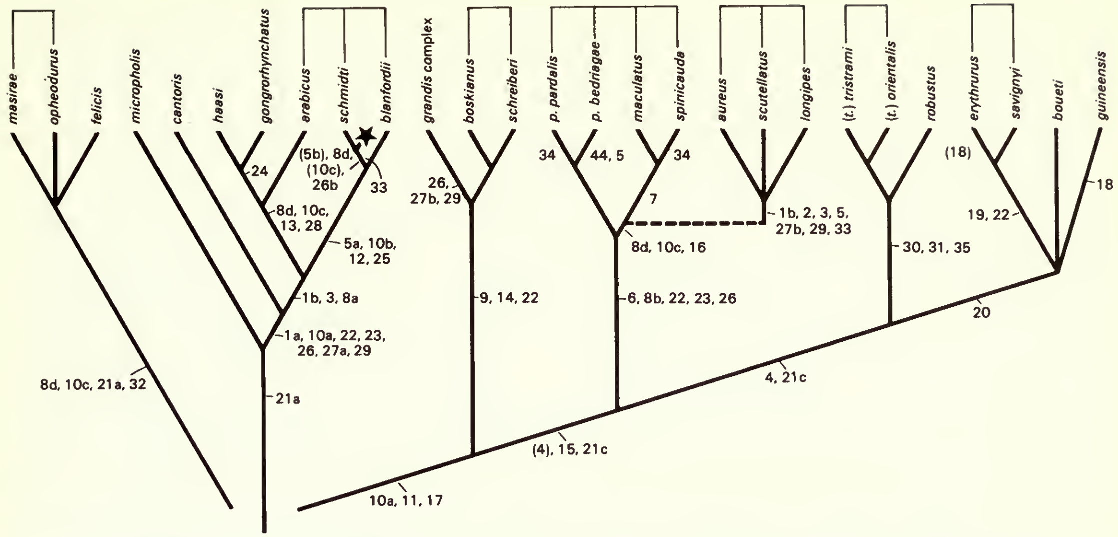
masirae
opheodurus
felicis
micropholis
cantoris
haasi
gongrorhynchatus
arabicus
schmidti
blanfordii
grandis complex
boskianus
schreiberi
p. pardalis
p. bedriagae
maculatus
spinicauda
aureus
scutellatus
longipes
(t.) tristrami
(t.) orientalis
robustus
erythrurus
savignyi
boueti
guineensis
★
24
(5b), 8d, (10c), 26b
33
8d, 10c, 13, 28
5a, 10b, 12, 25
1b, 3, 8a
1a, 10a, 22, 23, 26, 27a, 29
21a
8d, 10c, 21a, 32
26, 27b, 29
9, 14, 22
34
44, 5
34
7
8d, 10c, 16
6, 8b, 22, 23, 26
1b, 2, 3, 5, 27b, 29, 33
30, 31, 35
(18)
19, 22
18
20
4, 21c
(4), 15, 21c
10a, 11, 17

Fig. 9 Tentative hypothesis of the relationships of the species of *Acanthodactylus.* Figures refer to derived characters listed in Tables 8 and 9. Lines above species names join forms that have a very close overall resemblance. ★-indicates alternative position for the *A. scutellatus* group (*A. aureus, A. scutellatus* and *A. longipes*).

A number of *Acanthodactylus* species share a distinctive hemipenial structure which incorporates two derived features not found elsewhere: the medial clavula is narrow and pointed with a ⊰-shaped cross section (11) and the most medial connector on the lateral side is often thickened (17); in addition there is moderate asymmetry of the armature (10a). This pattern occurs in *A. boskianus, A. schreiberi,* the *A. grandis* complex, *A.* (*t.*) *tristrami, A.* (*t.*) *orientalis, A. robustus, A. erythrurus, A. savignyi, A. boueti* and *A. pardalis.* It seems probable that these forms constitute a monophyletic group in Ashlock's (1974) sense within *Acanthodactylus.* Among them *A. boskianus, A. schreiberi* and the *A. grandis* complex all have a reduced proximal lip to the medial branch of the hemipenial sulcus (9) and a lateral clavula that is complexly lobed (14). Within this trio, *A. boskianus* and *A. schreiberi* may well be sister species, for some populations are extremely similar. *A. grandis* shows conflict of evidence as to its relationships. It has some similarity in derived features to members of the *A. cantoris* group, viz. high number of ventral scales (26) which are tessellated (27b) and four longitudinal rows of scales along the fingers (29b). However, weighting criteria (especially frequent occurrence in groups not closely related to *Acanthodactylus*) suggest these features are relatively weak indicators of relationship, whereas it has been argued (p. 329) that most of the conflicting hemipenial features (9, 11, 14, 17) that ally the *A. grandis* complex to *A. boskianus* and *A. schreiberi* are likely to be of greater reliability. Moreover, any detailed placement of the *A. grandis* complex in the *A. cantoris* group would involve additional homoplasies.

Members of the *A. tristrami* group share features not found elsewhere in the genus, viz. no keeling on the proximal, dorsal caudal scales (30), a short tail (31) and an often distinctive pattern (35). The very similar *A.* (*t.*) *tristrami* and *A.* (*t.*) *orientalis* could well be sister species. *A. robustus* has some features that suggest relationships elsewhere: subocular scale separated from the mouth (22), increased number of ventrals (26a) and an irregular fourth scale row on the fingers (29a), but none of these derived states is very strongly developed and all seem likely to be relatively weak indicators of relationship compared with those allying *A. robustus* with *A.* (*t.*) *tristrami* and *A.* (*t.*) *orientalis.*

The *A. tristrami* and *A. erythrurus* groups share some distinctive features, in particular a high number of presacral vertebrae (4) and fragmented first and fourth supraocular scales

(21c). Furthermore, some species of each have a lateral clavula that is bifurcate at its tip (15), so it seems reasonable to regard the two assemblages as closely related. The members of the *A. erythrurus* group are all generally similar and at least some individuals of all species have one or more azygos shields between the prefrontal scales (20) although this condition also occurs occasionally in other forms. It is suggested that *A. erythrurus* and *A. savignyi* are sister species on the evidence of their great similarity and frequent division of the frontonasal scale (19). They are also the only members of the group in which the subocular scale may be separated from the lip (22). *A. boueti* and *A. guineensis* both have distinctive features of their own (*A. boueti*—nine premaxillary teeth, fragmented parietal scales, small hemipenis (7), supraocular scales very fragmented (21d); *A. guineensis*—very asymmetrical hemipenis and armature (8d, 10c), lateral clavula rolled) but their precise relationships to each other and to *A. erythrurus* and *A. savignyi* are not clear. All *A. guineensis* examined (n = 20) have a peculiar arrangement of nasal scales (18) which occurs as a rarity in *A. erythrurus* (p. 296). However, this feature cannot be regarded as strong evidence of the close relationship of these species within the group, for its rarity in *A. erythrurus* raises the possibility that its apparent absence in *A. savignyi* and *A. boueti* may be due to inadequate sampling or to pseudoreversal (Arnold, 1981*a*).

The *A. pardalis* group seems likely to be a monophyletic assemblage on the basis of the strong overall similarity of its members. They also have more hemipenial asymmetry (8b or 8c) than the species placed in the *A. grandis* complex and the *A. boskianus, A. tristrami* and *A. erythrurus* groups, share a high incidence of interruption of the fifth sternal rib (6) and the number of ventral scales is also regularly high (26). The main reason for allying the *A. pardalis* assemblage with these groups is that the species with the least modified hemipenis, *A. pardalis,* has an armature just like the others with derived features 10a, 11 and 17. The absence of these features in the other two species in the *A. pardalis* group, *A. maculatus* and *A. spinicauda,* may be secondary, the result of the development of physical isolating mechanisms (p. 304). The *A. pardalis* group shares with the *A. tristrami* and *A. erythrurus* groups frequent bifurcation of the tip of the lateral clavula (15), some fragmentation of the supraocular scales (21b) and some tendency for high presacral vertebral counts (4). However, the last feature is not universal and the supraoculars are less broken up than in these forms. Because of this, the *A. pardalis* group is tentatively placed as a sister assemblage to them. Within the *A. pardalis* group, *A. maculatus* and *A. spinicauda* may be closely related having strongly asymmetrical hemipenes and armatures (8d, 10c) with the lateral clavula folded sideways (16).

Holophyly of the *A. scutellatus* group is supported by the close similarity of its members and their possession of a unique synapomorphy; premaxillary teeth reduced to five (2). Its members have several other derived features that occur elsewhere and these suggest conflicting hypotheses as to the closest relatives of the group. The main candidates are *A. schmidti,* particularly the populations in the United Arab Emirates that have little sexual variation in the number of presacral vertebrae, and all or part of the *A. pardalis* group. Derived features that these share with the *A. scutellatus* assemblage are set out in Table 10; the *A. grandis* complex shares a much smaller number, namely 26, 27 and 29. Most derived features, eleven, are shared with *A. schmidti* populations from the United Arab Emirates and only seven with the *A. pardalis* group of which no more than six occur in any one species. Thus on simple count of shared characters *A. schmidti* would be considered clearly the more likely sister taxon, but the likely quality of the features as indicators of relationship should also be taken into account. In general, the features shared with *A. schmidti* seem rather weak as they score badly on the weighting criteria listed by Arnold (1981*a*). For instance, numbers 3, 5, 6, 8d, 10c, 23, 26, 27, 29 and 33 occur in a number of other lacertid stocks; there are additional functional reasons for thinking 8d and 10c may have evolved more than once (p. 304); if the argument on p. 333 that the *A. grandis* complex is more closely related to the *A. boskianus* group than to the *A. cantoris* assemblage is accepted, then characters 23, 26, 27 and 29 must have evolved twice within *Acanthodactylus* and a third independent origin

Table 10 Comparison of derived features shared by the *A. scutellatus* group with *A. schmidti* and the *A. pardalis* group.

	A. schmidti			*A. pardalis* group	
	Main range	United Arab Emirates	*A. scutellatus* group	*A. pardalis*	*A. maculatus* *A. spinicauda*
1b Premaxilla narrow	+	+	+	–	–
3 Presacral vertebrae 23 or 24 in females	–	+	+	–	–
5b Little variation in number of presacral vertebrae	–	+	+	+	–
6 Fifth sternal rib often interrupted	–	–	+	+	+
8 Medial lobe of hemipenis very reduced	+	+	+	–	+
10c Medial side of armature very reduced	+	+	+	–	+
16 Lateral clavula folded to produce a ⊐-shaped cross section	–	–	+	–	+
23 High number of upper labials	+	+	+	+	+
26 Increased number of ventrals	+	+	+	+	+
27 Ventrals tessellated, at least at sides	+	+	+	–	–
29 Four scale rows on fingers	+	+	+	–	–
33 Young without stripes	+	+	+, –	–	–
Strong pectination on toes	+	+	+	–	–

would not seem unlikely; a number of features seem to be functionally related to the problems of living in the open, soft-sand habitats occupied by *A. schmidti* and the *A. scutellatus* group, this is true of 1b, 3, 29, 33 and strong pectination on the digits; the coercive selective forces likely to produce convergence of these features are discussed in the relevant character descriptions. Finally, two features, 3 and 5, are confined in *A. schmidti* to a very small part of the geographical range, the United Arab Emirates. The restricted distribution of these characters suggest they may well have developed independently within the species. If so, the number of features to be considered is reduced to nine. On the other hand the relationship of the *A. scutellatus* assemblage to the *A. pardalis* group is supported by an apparently unique hemipenial feature (16) and the high incidence of interrupted sternal ribs, a condition not found elsewhere in the genus. Assessing such conflicting evidence is inevitably difficult but, on balance, the author is inclined to believe that the *A. scutellatus* group is most closely related to the *A. pardalis* assemblage.

As stated, the members of the *A. opheodurus* group are placed together largely on the grounds of overall similarity which is especially marked between *A. opheodurus* and *A. felicis*. Shared derived features are 8d, 10c and in some individuals of each species 32a; none of these are unique to the group. Evidence for the inter-relationship of the species is conflicting: *A. felicis* and *A. opheodurus* share 5a and 22 while the latter species and *A. masirae* share 1 and 29, although 29 occurs only in a reduced form in *A. opheodurus* and only in a minority of individuals.

The lack of strong derived characters makes it difficult to relate the *A. opheodurus* group to other *Acanthodactylus*, but absence of a thickened hemipenial connector (17) suggests that it is not directly related to the *A. grandis–A. guineensis* sequence (see Fig. 9). Nor is it clear how this sequence relates to *A. micropholis* and the *A. cantoris* assemblage.

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Addendum

Since this paper was submitted for publication, I have had the opportunity to see the recent article on *Acanthodactylus* by Dr Alfredo Salvador. (1982). In the main, we are in agreement over species boundaries within the genus and a number of the divergencies that exist can be attributed to using different criteria for deciding if allopatric populations merit species status or not, always a rather subjective decision. These and other more important disagreements are briefly considered below.

1. The *A. yemenicus* group of Salvador is the same as the *A. opheodurus* group of Arnold (1980*b* and this paper) but with the addition of a new taxon, *A. yemenicus.* This form has much in common with *A. felicis.* Unlike the other members of the group, its specific status cannot be confirmed by sympatry, as its range is completely separate from the others. There are considerable differences between the two populations from which *A. yemenicus* has been described, Ta'izz and the Sheikh Osman-Aden area, even although these are only separated by some 130 km.

2. *A. erythrurus* group. Salvador treats *blanci* as a full species rather than a subspecies of *A. savignyi.* Given the differences between this form and typical *savignyi*, this course is not unreasonable.

3. *A. pardalis* group. *A. pardalis*, as understood here, is divided by Salvador into three full species: *A. p. pardalis* becomes monotypic as *A. pardalis, A. p. bedriagai* becomes *A. bedriagai* and the Moroccan population related to *bedriagai* becomes *A. busacki* n. sp. These forms overlap in many morphological features.

4. *A. tristrami* sens. lat. Salvador regards *A. tristrami*, in its wide sense, as consisting of two subspecies: *A. t. tristrami,* with which *A. t. orientalis* is synonymized, and *A. t. iracensis.* This contrasts with the arrangement adopted here where *orientalis* is regarded as separable from *tristrami* and *iracensis* is synonymized with *orientalis.* A careful examination of the types of all three forms and of most other available material convinces me that the latter course is more appropriate. *A. t. iracensis* cannot be separated from *orientalis* on the basis of the

features mentioned by Schmidt (1939), namely lower transverse dorsal count, less vivid colour pattern and more sharply pectinate toes; nor does it differ significantly in any of the other features investigated. On the other hand, typical *tristrami* differs from *orientalis*, including *iracensis*, not only in its larger size, more numerous dorsal scales and hemipenial structure, but usually also in its deeper snout with convex upper profile, absence of a denticulation on the anterior edge of the ear and virtual lack of pectination on the toes. In addition, the first supraocular is more fragmented (*tristrami*–n = 10, average number of fragments on each side 5.4, range 3–10; *orientalis*–n = 17, average number of fragments on each side 2.8, range 1–6).

5. *A. scutellatus* group. Salvador divides *A. scutellatus*, as understood here, into *A. scutellatus* in the east and *A. dumerilii* in the west. The two supposed species are said to approach each other in Mali and Algeria but not to integade. I have re-examined the BM(NH) material from Mali that Salvador assigns to *A. scutellatus* and *A. dumerilii* and can find no differences in the features that are said to separate them, namely transverse ventral count, snout shape and number of rows of supraciliary granules. Where *A. scutellatus* and *A dumerilii* approach each other around the Algerian-Tunisian border, I again find no consistent differences in snout shape as mentioned by Salvador, and although there are average differences in degree of fragmentation of the fourth supraocular scale, there is substantial overlap. I consequently regard the separation of *A. dumerilii* from *A. scutellatus* as unproven.

Salvador divides his *A. dumerilii* into two subspecies: *A. d. dumerilii* in Senegal, southwest Mauretania and Mali and *A. d. exiguus* in Algeria and Morocco. The former is said to have 12 instead of 14 longitudinal rows of ventral scales, two instead of one row of supraciliary granules and longer legs. In material I have examined, I find that two rows of supraciliary granules are often absent in the area where *A. d. dumerilii* is reported and leg length is variable. Furthermore, there is a very large intergrade area between the two subspecies where other characters vary clinally. It scarcely seems worth while naming such poorly defined entities, especially when *A. scutellatus* varies so substantially elsewhere in its large North African range and no subspecies names are assigned.

6. The diagnosis of *Acanthodactylus* given on p. 8 does not fully differentiate the genus from *Meroles* or *Eremias.*

Salvador, A. 1982. A revision of the lizards of the genus *Acanthodactylus* (Sauria: Lacertidae). *Bonn. zool. Monogr.* **16**: 1–167.

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Colin G. Ogden & Andjelija Živković

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Morphological studies on some Difflugiidae from Yugoslavia (Rhizopoda, Protozoa)

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Introduction

Recent studies (Ogden, 1979, 1980*a, b,* 1983; Ogden & Fairman, 1979) on the shell morphology of specimens belonging to the family Difflugiidae, have shown that detailed examination of these structures aid identification at the species level. It is now possible using the scanning electron microscope to demonstrate differences in shell structure and to examine more easily the type and arrangement of materials used in these complex constructions. Earlier workers were handicapped in similar examinations by the limited resolution of reflective optical microscopy. This made comparisons of shell structure difficult due to the different densities of the shell ranging from opaque to transparent, and sometimes the shape made a complete survey impracticable, ovoid or circular shells being particularly awkward. The present work is based on specimens collected in Serbia, Yugoslavia, from an area of peat bogs located on the high plateau at 1200 m, now submerged by the artificial lake 'Vlasina', which was formed by damming the river Vlasina and flooding a depression. A limnological study of this lake by Milovanović & Živković (1956) gives information relating to the chemical and biological conditions during the initial formation of this feature.

There are several reasons for our interest in the Difflugiidae of Yugoslavia, no previous records of testate amoebae are available for this region, there appears to be a similarity of this fauna with that reported from Africa by Gauthier-Lièvre & Thomas (1958) and specimens of the so-called 'cosmopolitan' species are available for comparison with those already described from the British Isles. Furthermore, the presence of several compressed species of *Difflugia* is unusual, as these forms appear to be rare.

Materials and methods

Samples were collected in September, 1947 from a pond 'Godžina bistrica' located at the

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margin of a peat bog, and preserved in formalin. The samples were divided into two in 1980, one half was deposited in the Zoology Department, British Museum (Natural History) and the other was retained in Yugoslavia. This report is based mainly on the BM(NH) specimens but reference is also made to those in the other sample. Selected shells from the sample were washed in several changes of distilled water, then individuals were prepared for scanning electron microscopy using the technique described by Ogden (1979). The prepared stubs were examined using a Cambridge Stereoscan S180 operating at 10 kV and the results recorded on Ilford HP5 film.

Systematic descriptions

The species of *Difflugia* are listed in alphabetical order, except for the new species which are described last and *D. gramen* which is described with *D. schurmanni* for comparative purposes. The single species of the genus *Cucurbitella* and two species of *Pontigulasia* are described after the species of *Difflugia*. The measurements for total body length includes aboral processes, unless otherwise stated, breadth and diameter of aperture are taken as the widest point, the latter is an internal measurement.

Genus ***DIFFLUGIA*** Leclerc, 1815

Difflugia acuminata Ehrenberg, 1838

A single specimen, 199 µm long, 85 µm in breadth, with an aperture diameter of 37 µm, was examined and seen to be identical to those already described (Ogden, 1979). Significantly the distinctive organic cement pattern of this species, a network in which each mesh is further divided by a smaller network, was present.

Difflugia acutissima Deflandre, 1931

DESCRIPTION. The shell is transparent, pyriform with the sides tapering evenly from about the mid-body region and terminating usually with a sharp point (Fig. 1a). It is composed mainly of flattish pieces of quartz to give a smooth surface, with organic cement sometimes seen as part of the shell matrix (Fig. 1c). The cement is usually in the form of a network about 400 nm in diameter with walls 200 nm thick, and each mesh is covered by a smooth membrane (Fig. 1d). The aperture is circular and surrounded by small to medium particles (Fig. 1b). One specimen had an oblique aperture and a misaligned aboral protuberance (Fig. 1e), the latter being only partially sealed (Fig. 1f), but was considered to agree with the general description of this species in all other respects.

MEASUREMENTS (in µm). Four specimens: body length 178–217, breadth, 80–107, diameter of aperture 47–51.

GEOGRAPHICAL DISTRIBUTION. Argentina (Dioni, 1970), Chad (Gauthier-Lièvre & Thomas, 1958), Congo (Chardez, 1964), Gold Coast, Morocco (Gauthier-Lièvre & Thomas, 1958), United States of America (Leidy, 1879), Venezuela (Deflandre, 1931).

REMARKS. This species was initially described by Deflandre (1931) who considered that it was distinct from *D. acuminata* and its varieties by the sharpness of the aboral extremity. It differs from *D. ventricosa,* also described by Deflandre (1926) from Venezuela, by having a much wider body and aperture. The general body dimensions are similar to those given for *D. distenda* by Ogden (1983), which was a variety of *D. acuminata* but this species is curved aborally to a small tubular horn. The problems of differentiating between species with aboral horns or spines are emphasized in two publications by Chardez (1961 & 1973), which show several figures supposedly pertaining to the same species. It is clear that concise specific

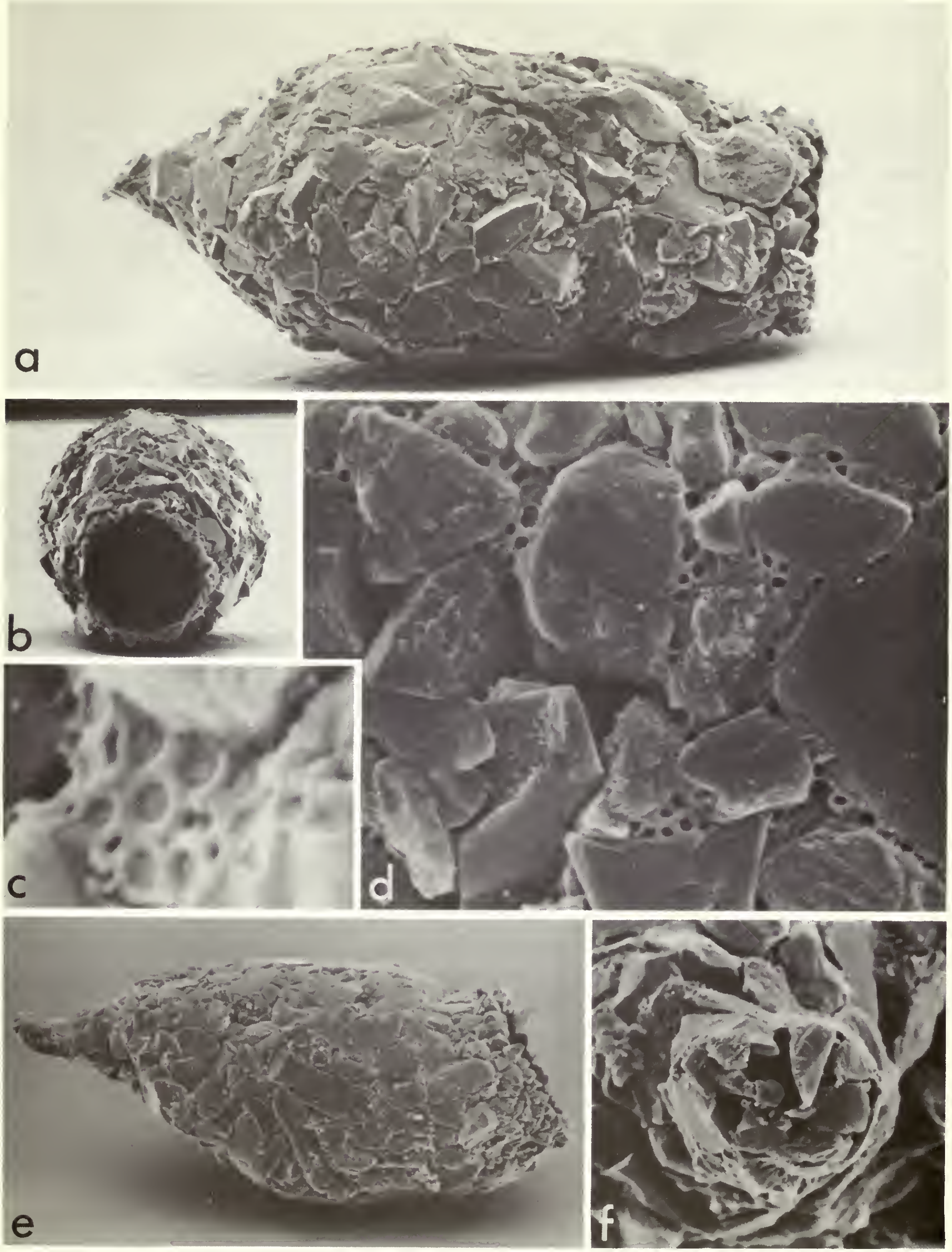

Fig. 1 *Difflugia acutissima*: a, lateral view × 600; b, apertural view × 360; c, detail of organic cement pattern × 14000; d, portion of shell surface to show organic cement between particles × 6600; e, specimen with oblique aperture and non-central aboral spine × 420; f, detail of partial closure at extremity of aboral spine × 1900.

identification of specimens must await morphogenetic evidence of natural variation of this feature within a species.

Difflugia bicornis Penard, 1890

Description. The shell is transparent, ovoid or spherical with usually two, but occasionally one aboral spines (Figs 2a & b). Of the three specimens examined only one had a single long aboral spine. The surface is rough, thin and composed of a mixture of small to medium particles of quartz, with the occasional addition of either a portion of diatom frustule or a siliceous flagellate cyst. Each aboral spine is roughly pointed and composed of small particles. A network of organic cement is sometimes seen between particles (Fig. 2d). It is in the form of a sheet with each mesh being separated by small walls, about 80 nm thick. The mesh is irregular, about 300–400 nm in diameter, and each enclosure often has a small inner circular wall with arms connecting it to the mesh wall (Fig. 2e). The aperture is usually circular and surrounded by a mixture of particles (Fig. 2c).

Measurements (μm). Three specimens: body length 75–85, breadth 39–53, diameter of aperture 19–23.

Geographical distribution. Germany (Penard, 1890; Jung, 1936), Guatemala, Mexico (Laminger, 1973), Switzerland (Penard, 1902).

Remarks. This species was initially described as a distinct species by Penard (1890) but was later considered (Penard, 1902) to be a small form of *D. elegans,* and he illustrated the variability of the shell in this form with several figures, including specimens with either one or two aboral spines. The specimens reported here have a fragile shell and are in good agreement with the original description of *D. bicornis,* the body lengths without the spines or horns being about 60 μm which is near to Penard's 50–60 μm. The contrast between these specimens and those of *D. elegans* studied recently (Ogden, 1979), which had robust shells and varied in body length between 113–158 μm, is marked. In the absence of information on other small forms identified as *D. elegans,* we have decided to use the earlier description of *D. bicornis* and consider the present specimens as a distinct species.

Difflugia bryophila (Penard, 1902)

A single specimen, 124 μm in body length, 53 μm broad with an aperture diameter of 17 μm. It was identical to those described by Ogden (1983).

Difflugia capreolata Penard, 1902

Description. The shell is opaque, thick, pyriform with a restriction of the neck at a position about one-third of the total body length, before it swells into the main body (Fig. 3a). It is composed of small to medium pieces of angular quartz, with small areas of organic cement as part of the matrix (Fig. 3c). This cement is in the form of a smooth sheet with irregular perforations (Fig. 3d), the reason that there is no apparent pattern to these perforations may be due to these areas being in thin strips rather than a more open arrangement. Each perforation has a mean diameter of 200 nm. The aperture is circular and surrounded by a regular distribution of medium particles (Fig. 3b).

Measurements (in μm). One specimen: body length 225, breadth 128, diameter of aperture 58.

Geographical distribution. Argentina (Dioni, 1970; Lena & Zaidenwerg, 1975), Germany (Schönborn, 1965), Russia (Kourov, 1925), Tunisia (Gauthier-Lièvre & Thomas, 1958), Sudan (Gauthier-Lièvre & Thomas, 1958), Switzerland (Penard, 1902).

Remarks. This species although it is large and has a distinctive outline, does not appear to be common and is rarely found in large numbers.

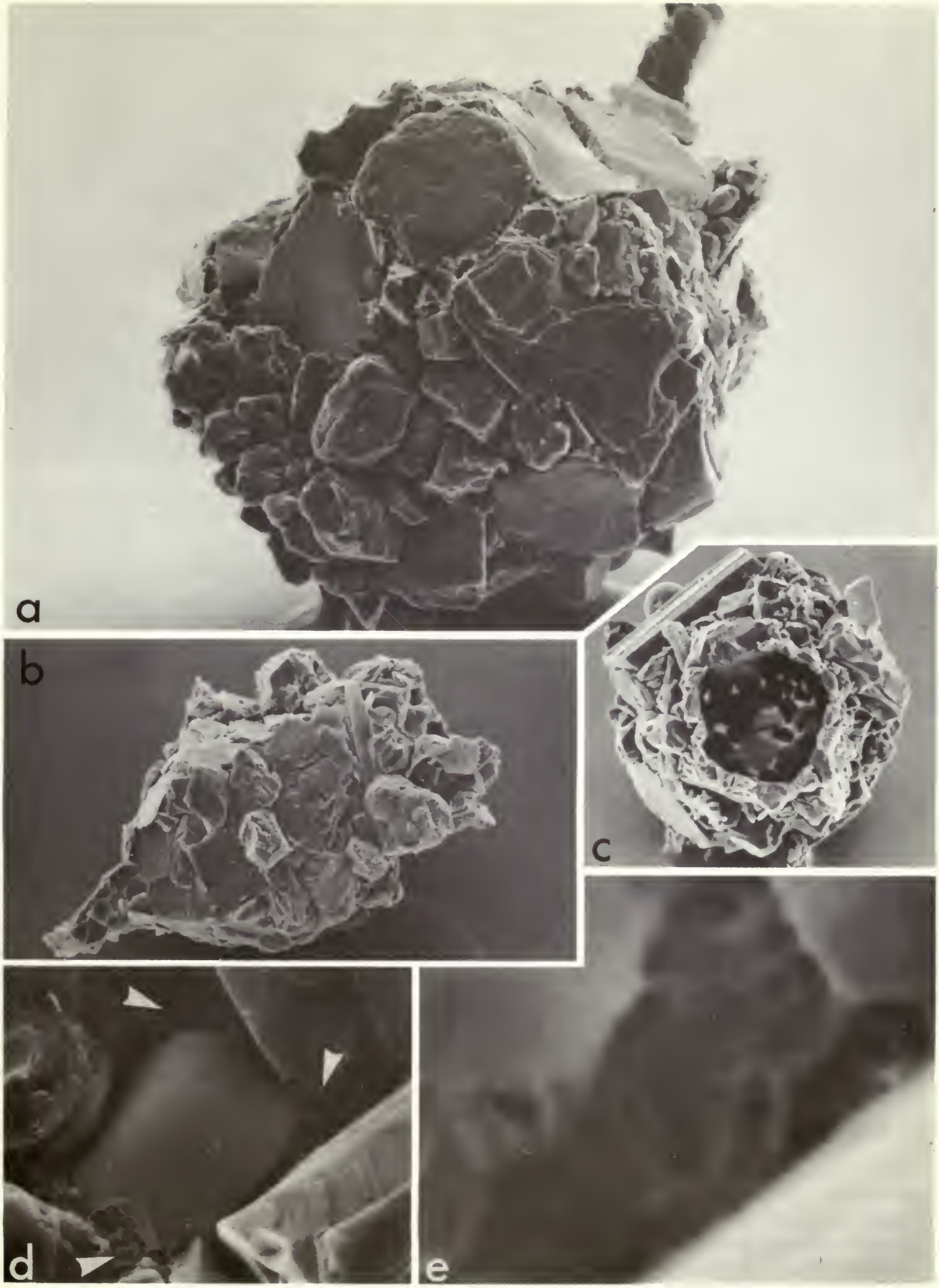

Fig. 2 *Difflugia bicornis*: a, lateral view of specimen with two aboral spines ×1400; b, lateral view of specimen with single aboral spine ×760; c, apertural view ×820; d, portion of shell surface to illustrate the organic cement (arrowed) ×7500; e, detail of organic cement ×35000.

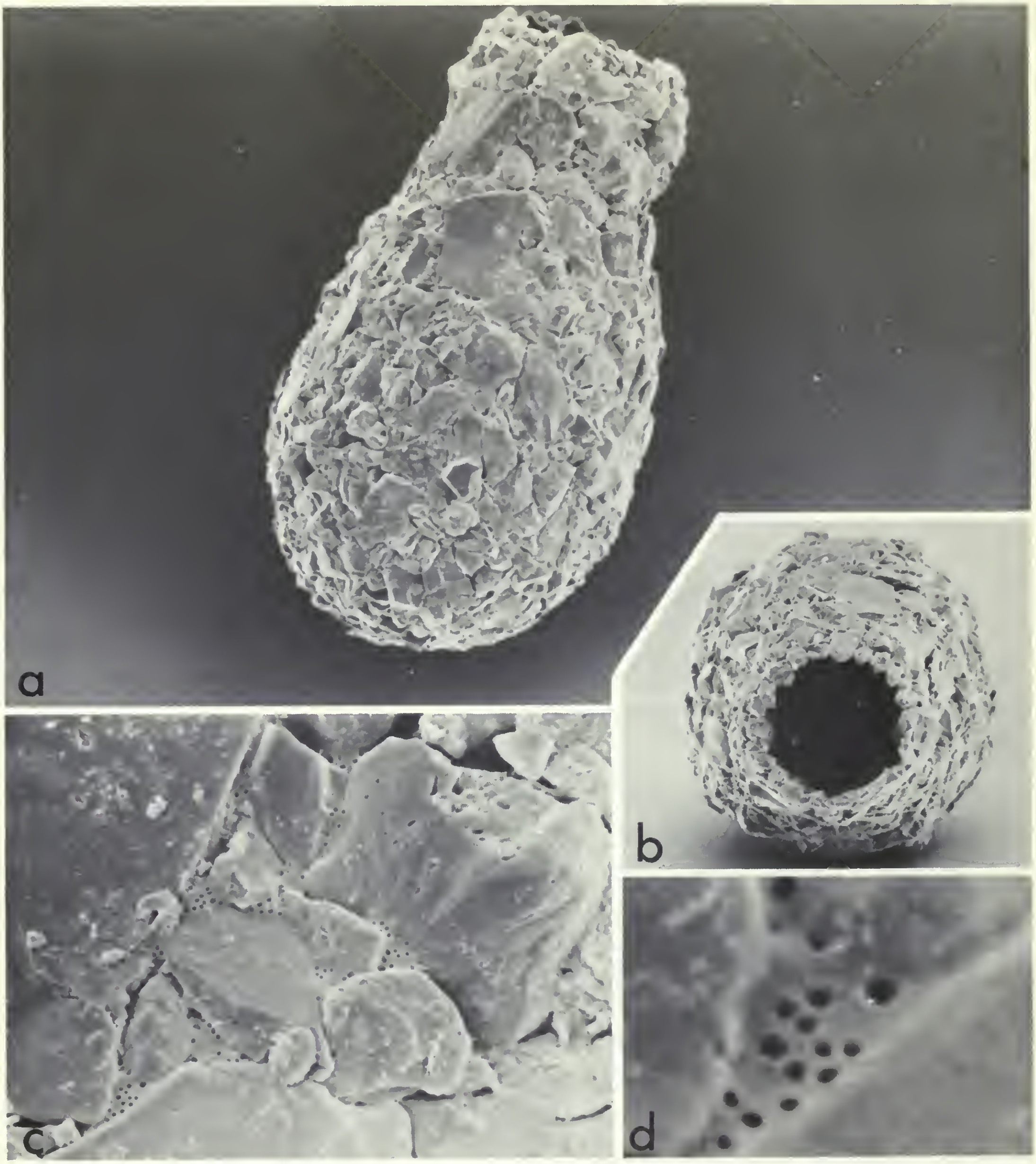

Fig. 3 *Difflugia capreolata*: a, lateral view ×400; b, apertural view ×340; c, shell surface showing small areas of organic cement ×3000; d, detail of organic cement pattern ×13000.

Difflugia corona Wallich, 1864

Description. The shell is brown, spherical or ovoid with distinct cone-like spines projecting from the aboral half of the body (Fig. 4a–d). The main body is composed of a mixture of small to medium particles of quartz arranged to give a relatively smooth shell. The spines are randomly arranged, varying between two and eight in number, made of small particles and are usually finely pointed. Organic cement in the form of a network is sometimes seen where particles meet. The aperture is circular and surrounded by a distinct denticular collar. There

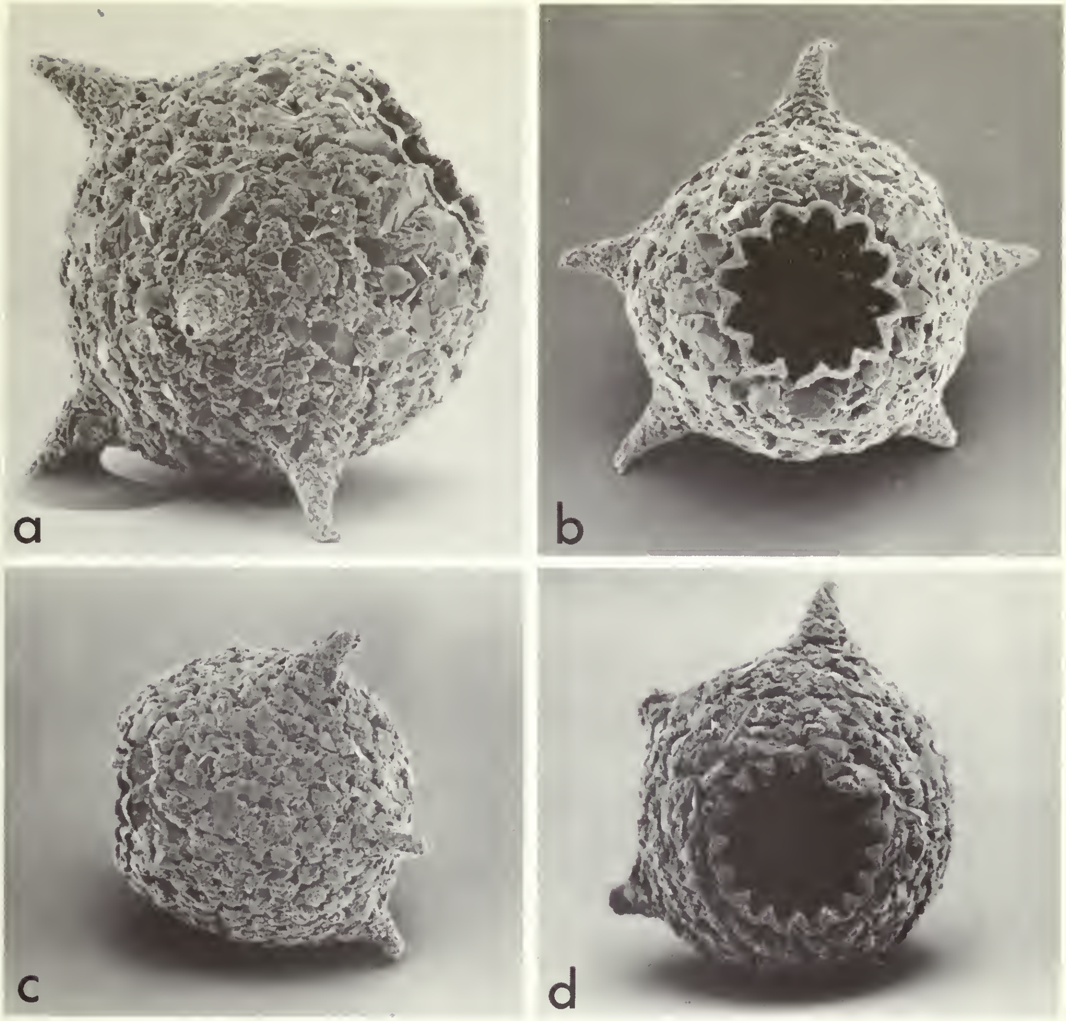

Fig. 4 *Difflugia corona*: a, lateral view of specimen with six spines ×430; b, apertural view of a, note the regular arrangement of twelve teeth ×330; c, lateral view of another specimen ×240; d, apertural view of c, to show sixteen thickened teeth ×240.

are usually between ten to twelve tooth-like projections, although one specimen in the present sample had sixteen (Fig. 4d). They are arranged evenly, usually being finely pointed, but as seen in Fig. 4d compression of the teeth makes the projections thicker and the outer curvature of the collar more rounded.

MEASUREMENTS (in µm). Fourteen specimens: body length 126–190, breadth 126–177, diameter of aperture 53–86.

GEOGRAPHICAL DISTRIBUTION. Algeria (Gauthier-Lièvre & Thomas, 1958), Argentina (Boltovskoy & Lena, 1974; Lena & Ziadenwerg, 1975; Vucetich, 1970), Austria (Laminger, 1975), Belgium (Chardez, 1961, 1980), Brazil (Green, 1975), British Isles (Ogden & Hedley, 1980; Wallich, 1864), Chad (Gauthier-Lièvre & Thomas, 1958), Congo (Chardez, 1964; Gauthier-Lièvre & Thomas, 1958), Czechoslovakia (Ertl, 1965), Germany (Penard, 1890), Hungary (Bereczky, 1973), India (Wallich, 1864), Java (Bartoš, 1963), Netherlands (Hoogenraad & Groot, 1940), Roumania (Godeanu *et al.,* 1973), Russia (Kourov, 1925),

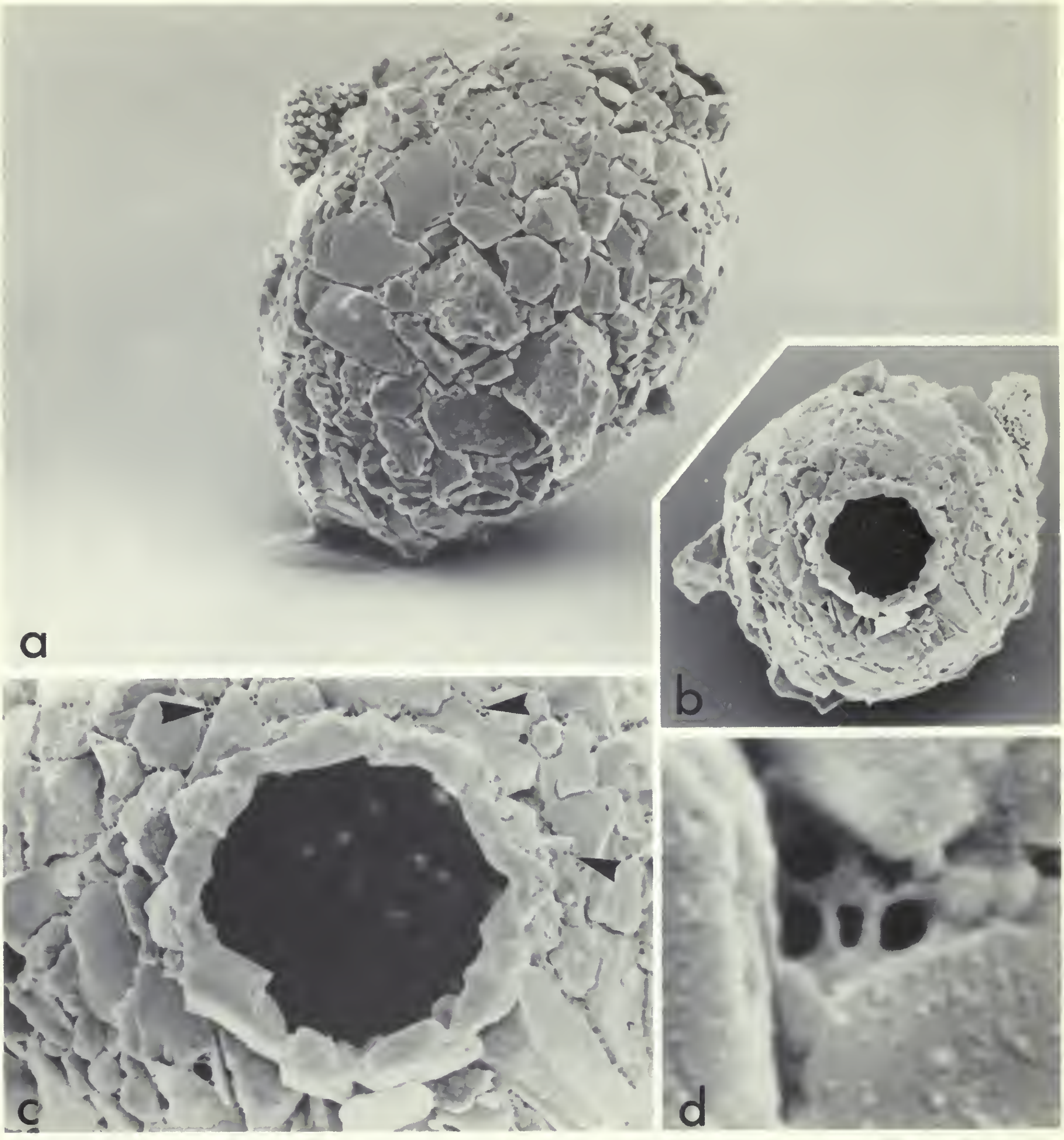

Fig. 5 *Difflugia difficilis*: a, lateral view ×950; apertural view ×760; c, detail of aperture to show short collar and organic cement (arrowed) between particles ×2100; d, detail of organic cement ×18000.

Senegal, Sudan and West Africa (Gauthier-Lièvre & Thomas, 1958), South Africa (Oye, 1931), Switzerland (Penard, 1902), United States of America (Leidy, 1879).

REMARKS. This species is truly 'cosmopolitan' having been reported from most continents, but these sightings are probably due to the ease in observing the prominent features of this large, distinctive shell in any sample. Although Jennings (1916, 1937) showed that variation of both teeth and spines occurred under cultural conditions, subsequent authors have continued to designate forms and varieties based on these structures. It could be argued that Jenning's observations were made on rough cultures and that clonal cultures would behave differently, or that the medium used was limiting in some way. Nevertheless, some of the reported features could easily be considered to represent natural variation.

Difflugia decloitrei Godeanu, 1972

A single specimen similar to those recently described by Ogden (1983) was found. It is possibly an encysted form as the aperture was blocked with several flat pieces of quartz bound by organic cement.

Measurements (in μm). One specimen: body length 79, breadth 52, diameter of aperture 22.

Difflugia difficilis Thomas, 1954

Description. The shell is transparent, ovoid, thin with a small apertural collar (Fig. 5a). It is composed of small to medium pieces of angular quartz arranged to make a relatively smooth surface, with the occasional projection of some particles. A network of organic cement is frequently seen as part of the shell matrix (Fig. 5c). The mesh of this network is open, each opening being about 350 nm wide with dividing walls 200 nm thick (Fig. 5d). A short collar made mainly of regularly arranged smallish particles, surrounds the circular aperture (Figs 5b & c).

Measurement (in μm). One specimen: body length 81, breadth 56, diameter of aperture 18.

Geographical distribution. Algeria (Gauthier-Lièvre & Thomas, 1958), Argentina (Lena & Zaidenwerg, 1975), Congo (Chardez, 1964), France (Thomas, 1954), Ivory Coast (Gauthier-Lièvre & Thomas, 1958), Roumania (Godeanu *et al.,* 1975), Sudan (Gauthier-Lièvre & Thomas, 1958).

Remarks. This specimen has similar dimensions to those given for *D. difficilis* and *D. kabylica* by Gauthier-Lièvre & Thomas (1958). It differs from *D. kabylica* in having a smaller aperture which does not have a flattened irregular outline. It is most similar to *D. difficilis,* although it does not have 'une excoissance peu proéminente' as initially described by Thomas (1954). However this species was later reported (Gauthier-Lièvre & Thomas, 1958) to vary a great deal in body outline and often the aboral protuberance is absent. The feature that is characteristic of this species is the small collar and in the absence of further specimens the present specimen is considered to be *D. difficilis.*

Difflugia gramen

See p. 357.

Difflugia labiosa Wailes, 1919

Two specimens of this species identical to those recently redescribed by Ogden (1983) were found.

Measurements (in μm). Two specimens: body length 176 & 177, breadth 111, diameter of aperture 45 & 52.

Difflugia lata Jung, 1942

Difflugia oblonga forma *lata* Jung, 1942

Description. The shell is opaque, pyriform having a rough surface composed of a mixture of mainly small to medium pieces of quartz, with an occasional large particle added (Fig. 6a). One specimen has a curved or malformed aboral extremity (Fig. 6c), but in all other respects is similar to the original description. Organic cement in the form of a network is seen as part of the shell matrix (Fig. 6d). The mesh of the network is open and has a mean diameter of 350 nm with walls 200 nm thick, although the walls often fuse to give larger areas of cement (Fig. 6e). The aperture is circular and surrounded by both small and medium particles arranged to give a somewhat irregular outline (Fig. 6b).

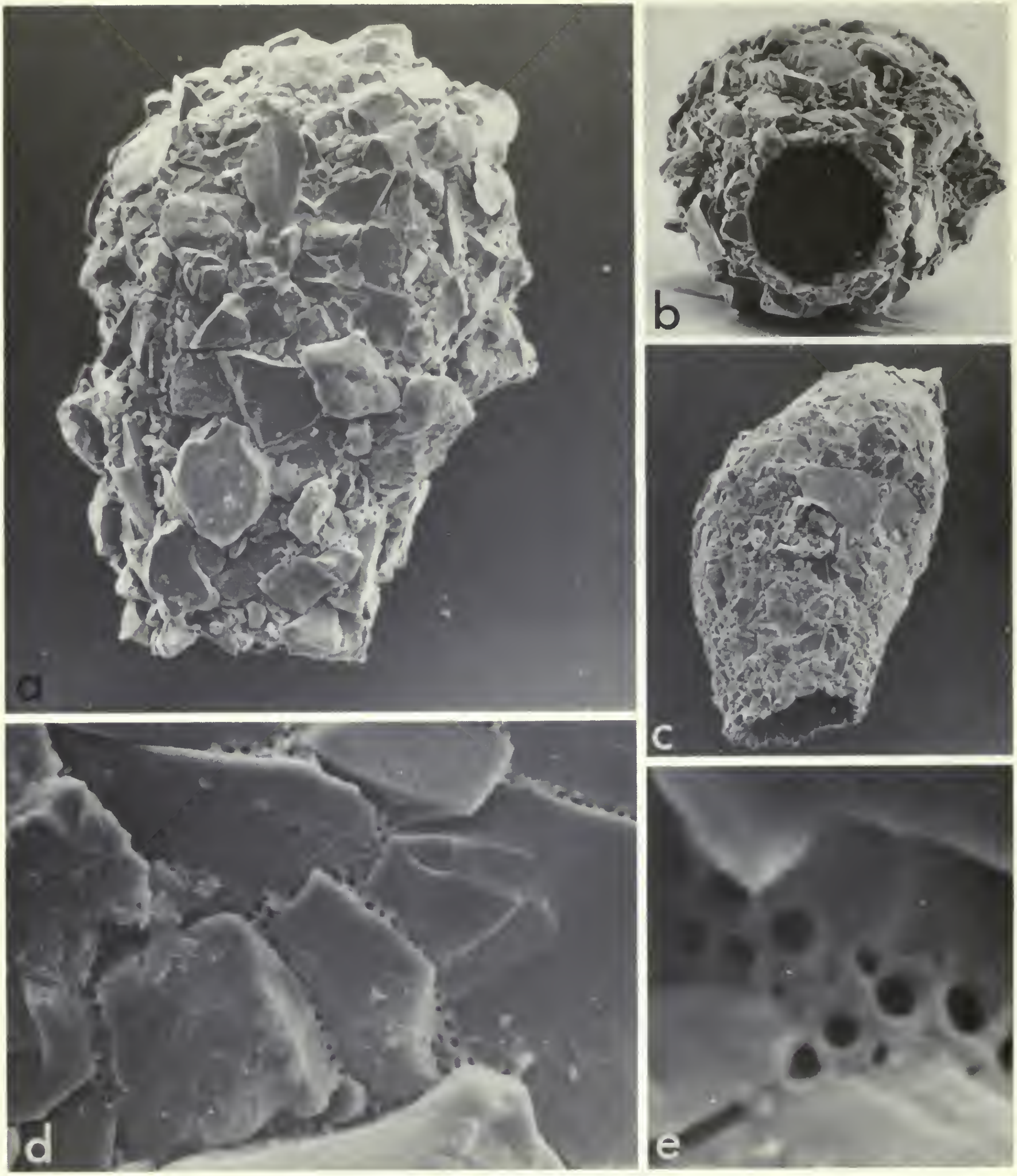

Fig. 6 *Difflugia lata*: a, lateral view ×590; b, apertural view ×420; c, specimen with malformed aboral extremity ×400; d, shell surface with organic cement as part of matrix ×3600; e, detail of organic cement ×13500.

Measurements (in µm). Two specimens: body length 137 & 149, breadth 90 & 103, diameter of aperture 42 & 46.

Geographical distribution. Chile (Jung, 1942).

Remarks. This species is known apparently only from the initial description (Jung, 1942) as a new form of *D. oblonga*. Although measurements are not given in the original text, from

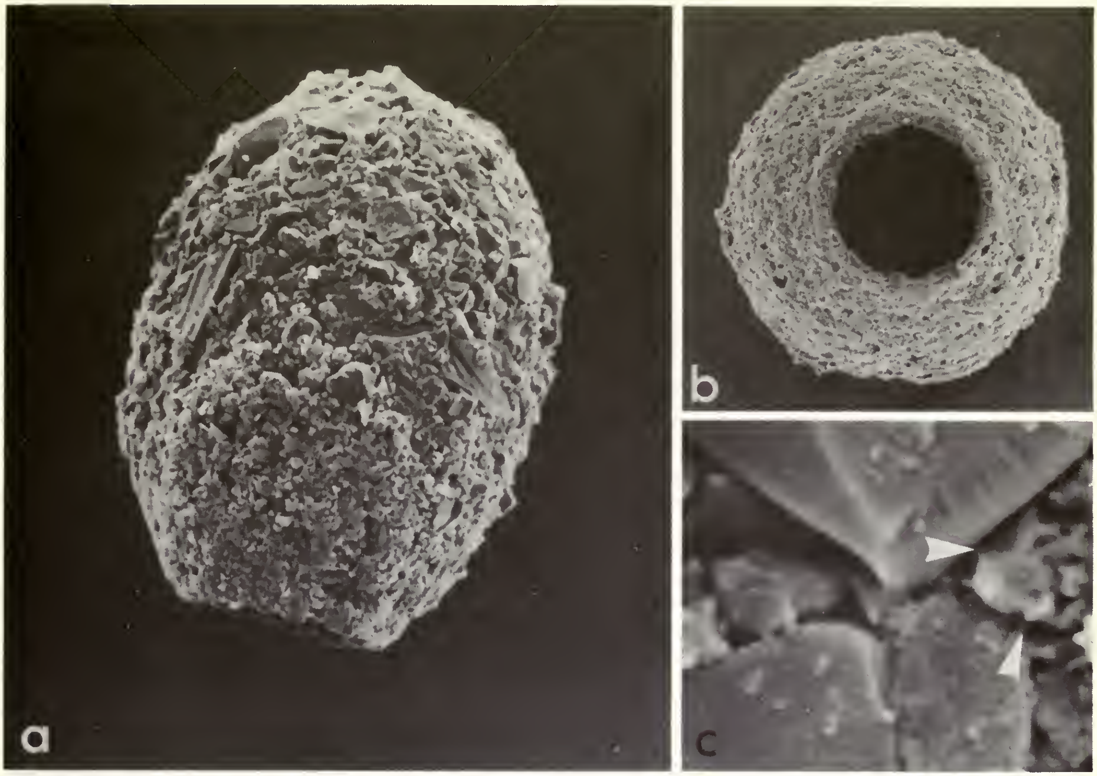

Fig. 7 *Difflugia levanderi*: a, lateral view ×730; b, apertural view ×530; c, portion of shell surface with organic cement (arrowed) ×7000.

the figure these are estimated to be body length 157 μm, breadth 81 μm and diameter of aperture 43 μm, which agree well with the present specimens. Note that our Fig. 6c compares well with that given by Jung (1942). This species is considered to be distinct from *D. oblonga* (see Ogden, 1979) in its stout pyriform body, wide aperture and organic cement pattern.

Difflugia levanderi Playfair, 1918

Description. The shell is ovoid or almost spherical, composed of flattish and angular pieces of quartz to give a regular outline (Fig. 7a). The particles appear to overlap and produce a robust structure with a network of organic cement, which is seen infrequently, binding the particles (Fig. 7c). Details of the surface are restricted because all the examined specimens have a slight covering of small debris, this latter material is clearly no part of the shell structure. The aperture is circular, well defined and surrounded by small particles (Fig. 7b).

Measurements (in μm). Five specimens: body length 95–104, breadth 76–92, diameter of aperture 32–40.

Geographical distribution. Algeria (Gauthier-Lièvre & Thomas, 1958), Australia (Playfair, 1918), Chile (Jung, 1942), Morocco and Tunisia (Gauthier-Lièvre & Thomas, 1958).

Remarks. The descriptions of both Levander (1894) and Playfair (1918) refer to specimens having a similar shape but differing in size and composition. The larger being robust with a coarse appearance, whilst the smaller had a chitinous shell with a scattering of particles. Unable to differentiate them Playfair (1918) described them as a new species *D. levanderi*.

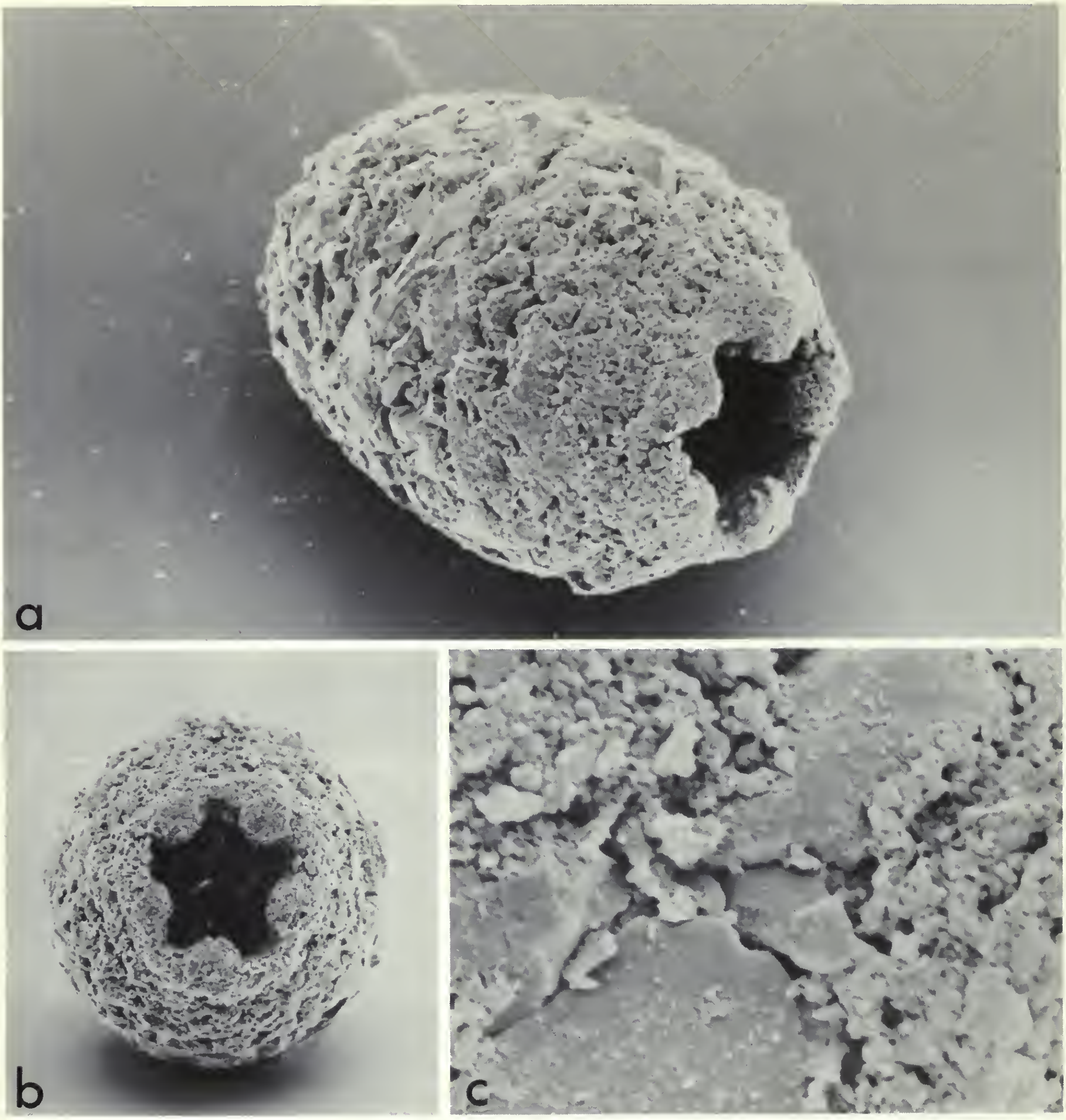

Fig. 8 *Difflugia lismorensis*: a, latero-apertural view ×640; b, apertural view to illustrate the thickened teeth and collar ×470; c, part of shell surface with overlay of extraneous material ×3400.

Fortunately, he created a precedence by initially describing the larger specimens, which are now considered to represent *D. levanderi*. Specimens similar to *D. levanderi* except for being smaller and having a thin shell whose particles did not overlap, were described by Godeanu (1972) as a new species *D. decloitrei*, and these are considered to be identical to the smaller animals described by Levander (1894), Playfair (1918) and redescribed by Ogden (1983).

Difflugia lismorensis Playfair, 1918

Difflugia lismorensis var. *quinquelobata* Gauthier-Lièvre & Thomas, 1958
Difflugia lismorensis var. *elongata* Gauthier-Lièvre & Thomas, 1958

DESCRIPTION. The shell is either elongate or ovoid, thick, composed of small to medium pieces of quartz arranged to give a rough surface (Fig. 8a). All the specimens examined had a proportion of the surface covered with an overlay of small extraneous material (Fig. 8c), nevertheless, the portions of actual surface visible had only strands of organic cement as part of the shell matrix. The aperture has five lobes which are equally spaced, strong, blunt, tooth-like extensions (Fig. 8b). Often the strengthening around these lobes, usually with small particles, gives it a collar-like appearance (Fig. 8b).

MEASUREMENTS (in μm). Three specimens: body length 132–144, breadth 96–104, diameter of aperture 36–45.

GEOGRAPHICAL DISTRIBUTION. Argentina (Vucetich, 1970), Australia (Playfair, 1918), Brazil (Green, 1973), Chad (Gauthier-Lièvre & Thomas, 1958), Congo (Chardez, 1964; Gauthier-Lièvre & Thomas, 1958), Gold Coast, Morocco and Sudan (Gauthier-Lièvre & Thomas, 1958).

REMARKS. Playfair (1918) described *D. lismorensis* as having an ovoid or sub-globular shell with a six-lobed aperture, and added two varieties *trilobulata* and *crucifera* which had three and four lobes respectively. Since that time two more varieties with five lobes, from Africa, have been described by Gauthier-Lièvre & Thomas (1958). They suggested the name *quinquelobata* for the ovoid variety and *elongata* for the specimens with an elongate body, the former has subsequently been reported again in Africa by Chardez (1964). Vucetich (1970) after examining about 50 specimens with seven lobes from Argentina, concluded that these were otherwise identical with *D. lismorensis* and she did not consider that differences in the number of lobes warranted specific designation. Until examples of this species from Australia, Africa and South America are compared, we agree with Vucetich (1970) that her specimens, plus those of Gauthier-Lièvre & Thomas are best described as *D. lismorensis.*

Difflugia lithophila (Penard, 1902), Gauthier-Lièvre & Thomas, 1958

Difflugia hydrostatica var. *lithophila* Penard, 1902

A single specimen identical to that described by Ogden & Hedley (1980) was examined. It is slightly smaller than previous records being 93 μm in body length, 67 μm breadth and having an apertural diameter of 32 μm; however, it is proportionally similar. African specimens appear to have a larger range of body length, 100–170 μm (Gauthier-Lièvre & Thomas, 1958), to those from Europe 99–140 μm (Penard, 1902; Thomas, 1954).

Difflugia lucida Penard, 1890

A single specimen was examined, it measured 61 μm in body length, 39 μm broad, 19 μm depth with an aperture diameter of 22 μm. Although slightly smaller than those examined in an earlier study (Ogden, 1983) it was otherwise identical.

Difflugia manicata Penard, 1902

Two specimens 76 & 78 μm long, 39 & 43 μm in breadth, with aperture diameters of 14 & 17, were examined and found to be identical to those recently redescribed by Ogden (1983).

Difflugia mica Frenzel, 1892

DESCRIPTION. The shell is brownish, spherical or ovoid sometimes with a shallow apertural collar (Fig. 9a). It is composed of flattish pieces of quartz arranged to give a relatively smooth surface, although one specimen has most of the surface obscured by extraneous material. Organic cement is seen infrequently between particles but is more evident around the aperture. The cement around the aperture is apparent as a thin layer on the surface of some outer particles (Fig. 9c), but is a concentration of strands, some apparently fused, on the

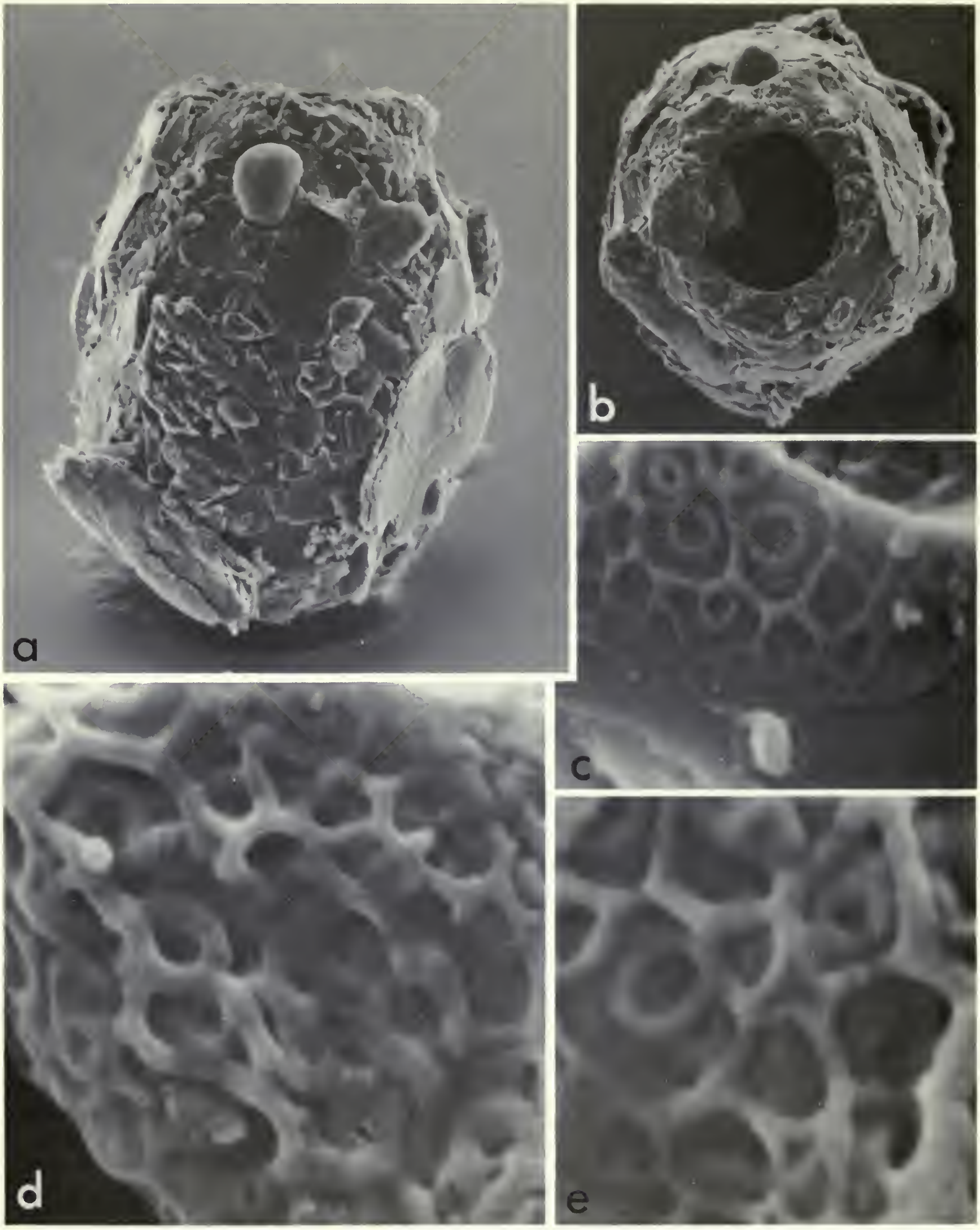

Fig. 9 *Difflugia mica*: a, lateral view showing the arrangement of flattish particles ×1400; b, apertural view ×1100; c, organic cement at outer limit of apertural concentration ×17000; d, concentration of organic cement on apertural lip, note the fusion of some strands ×20000; e, general appearance of organic cement network ×29000.

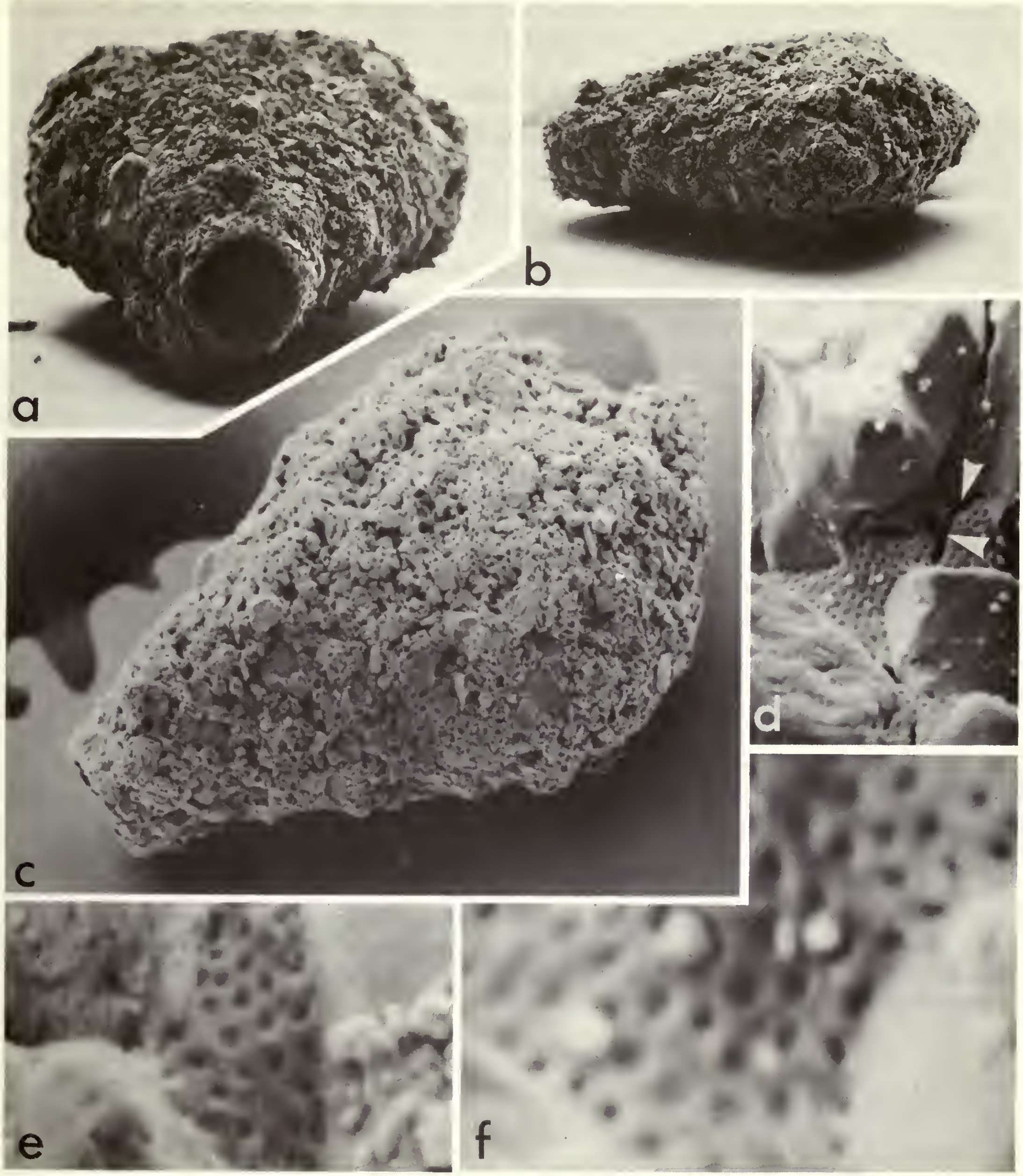

Fig. 10 *Difflugia nodosa*: a, apertural view ×270; b, view to illustrate lateral compression ×160; c, lateral view showing the lateral wings and aboral protuberance ×970; d, portion of shell surface close to aperture, note that the organic cement is torn (arrowed) ×4600; e, & f, detail of organic cement pattern ×14000 & ×21000.

apertural lip (Fig. 9d). The general structure is of a network with an irregular mesh about 300 to 500 nm in diameter, with dividing walls about 100 nm thick (Fig. 9e). The aperture is circular, well defined, usually with an organic margin and sometimes with a collar (Fig. 9b).

MEASUREMENTS (in µm). Two specimens: body length 55 & 60, breadth 46 & 55, diameter of aperture 19 & 18.

Remarks. These specimens are in good agreement with the description given by Ogden (1983). They are described again here to include information of the organic cement pattern.

Difflugia microclaviformis (Kourov, 1925)

The two specimens examined here fall within the range of body lengths given by Kourov (1925) of 139–160 μm, their respective measurements are:— body length 141 & 163 μm, breadth 66 & 75 μm and diameter of aperture 19 & 21 μm. Furthermore, they are in good agreement with the recent redescription of slightly larger specimens given by Ogden (1983).

Difflugia nodosa (Leidy, 1879) comb. nov.

Difflugia pyriformis var. *nodosa* Leidy, 1879 and in Penard, 1902
Difflugia oblonga var. *nodosa* Leidy, 1879 in Gauthier-Lièvre & Thomas, 1958

Description. The shell is thick, opaque, pyriform with the main body compressed to give two large lateral wings and an aboral extension or protuberance (Figs 10b & c). It is composed of a mixture of various sized pieces of quartz, which unfortunately in the present specimen is overlaid with debris. Nevertheless, some organic cement was observed close to the aperture (Fig. 10d); it is in the form of a network with the open mesh having a mean diameter of 200 nm and walls 200 nm thick (Figs 10e & f). The aperture is circular and surrounded by a regular arrangement of small particles (Fig. 10a).

Measurements (in μm). One specimen: body length 367, breadth 241, depth 140, diameter of aperture 53.

Geographical distribution. Algeria (Gauthier-Lièvre & Thomas, 1958), Belgium (Chardez, 1980; Chardez & Gaspar, 1976), Congo (Gauthier-Lièvre & Thomas, 1958), Germany (Laminger, 1973; Schönborn, 1962), Ivory Coast (Gauthier-Lièvre & Thomas, 1958), Netherlands (Hoogenraad & Groot, 1940), Roumania (Godeanu *et al.,* 1973), Russia (Kourov, 1925), Sudan (Gauthier-Lièvre & Thomas, 1958), United States of America (Leidy, 1879).

Remarks. This species has consistently been described as a variety of *D. oblonga*, initially Leidy (1879) remarked that it was a 'striking variety' distinguished by its unusually large size, compressed body and three conical eminences which varied a great deal in their development. Although Leidy (1879) reported it as being abundant on one particular occasion, so that one drop of ooze contained several dozen individuals, since that time no other reports have been so fruitful with specimens. Nevertheless, we consider that this variety is best treated as a distinct species which differs from the typical *D. oblonga* in the features described above and the organic cement pattern.

Difflugia oblonga Ehrenberg, 1838

Two specimens with the typically rough shell recently redescribed by Ogden & Fairman (1979) were examined; they measured: body length 232 & 263 μm, breadth 112 & 109 μm and diameter of aperture 46 & 41 μm.

Difflugia parva (Thomas, 1954)

The specimens of this species agree well with the redescription given by Ogden (1983) having a relatively smooth shell and areas of organic cement as part of the shell matrix; body length 143–203 μm, breadth 78–94 μm and diameter of aperture 24–32 μm.

Difflugia pristis Penard, 1902

Four specimens, body length 37–62 μm, breadth 27–38 μm and diameter of aperture 13–16 μm, having shells composed mainly of quartz particles but with some added diatom frustules, were examined.

Difflugia pulex Penard, 1902

Two small ovoid specimens, body length 30 & 32 μm, breadth 22 & 24 μm with diameter of aperture 10 & 11 μm were examined.

Difflugia rubescens Penard, 1891

Two specimens, body length 5 & 62 μm, breadth 34 & 40 μm and diameter of aperture 15 μm were examined.

Difflugia gramen Penard, 1902

Description. The shell is transparent or light brown, spherical tapering towards the aperture (Fig. 11a). It is composed of a mixture of small to medium pieces of quartz, bound by an organic cement network (Fig. 11c). A ring of small pores surrounds the aperture (see Ogden, 1980b) which is trilobed and bordered by an irregular raised rim (Fig. 11b).

Measurements (in μm). See Table 1.

Remarks. A brief description of this species is included so that a direct comparison can be made with specimens of *Difflugia schurmanni* Oye, 1932 described below.

Table 1 Range of measurements (in μm) of four ovoid species of *Difflugia.*

	n		Length (L)	Breadth (B)	Diameter of aperture (da)	B/L	da/L	da/B
D. achlora	2	(E)	49–54	43–46	16–17			
D. schurmanni	20	(Y)	50–70	36–52	18–26	0·74±0·05	0·35±0·04	0·48±0·03
D. gramen	24	(Y)	69–90	51–81	26–32	0·84±0·08	0·36±0·03	0·44±0·04
D. gramen	35	(E)	89–117	70–112	23–39	0·96±0·07	0·34±0·04	0·36±0·03
D. lobostoma	44	(E)	123–186	106–166	32–60	0·87±0·06	0·29±0·03	0·33±0·02

n = number of specimens; E = Norfolk, England (see Ogden, 1980*b*); Y = Yugoslavia (present work)

Difflugia schurmanni Oye, 1932

Description. The shell is transparent, elongate ovoid, tapering equally to the aperture and aboral extremity (Fig. 11d). It is composed mainly of flattish pieces of quartz arranged to give a smooth and rather fragile appearance. The particles are bound by organic cement, similar to that described for *D. gramen,* but because the particles fit closely together cement is not seen as frequently as in that species. The aperture is trilobed with the dividing projections less pronounced in apertural view (Fig. 11e) compared with those of *D. gramen,* and this gives it a more open outline especially as the shell has a smaller breadth (see Table 1). In addition, the surrounding ridge is often not as well defined although in lateral view the lobes are more prominent (Fig. 11d). A ring of small pores surrounds the aperture, similar to those described for *D. gramen* (see Ogden, 1980*b*).

Measurements (in μm). See Table 1.

Geographical distribution. Brazil (Green, 1975), Congo (Gauthier-Lièvre & Thomas, 1958), Guatemala (Laminger, 1973a), Senegal (Gauthier-Lièvre & Thomas, 1958), South Africa (Oye, 1932), Sudan (Gauthier-Lièvre & Thomas, 1958).

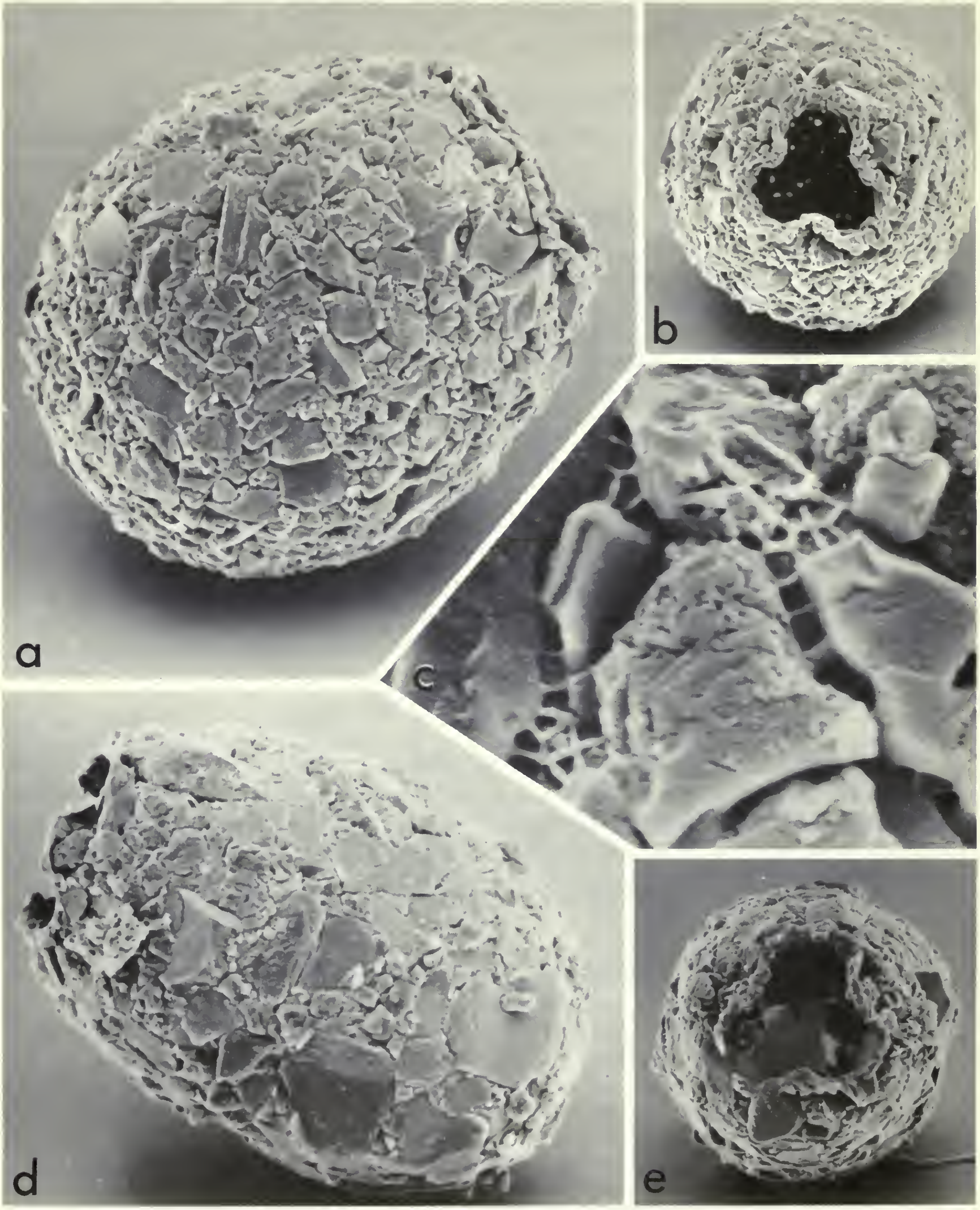

Fig. 11 *Difflugia gramen*: a, lateral view ×1000; b, apertural view, note the small aperture opening but well defined surrounding ridge ×610; c, detail of organic cement pattern ×7500 *Difflugia schurmanni*; d, lateral view, note the different arrangement of particles and defined apertural lobes ×1500; e, apertural view to illustrate wide opening and less pronounced ridge ×1000.

REMARKS. Reports of this species appear to be confined to tropical countries, but this may be due to it being reported elsewhere as *D. gramen.* The measurements of specimens for the three similar species, *D. achlora, D. gramen* and *D. lobostoma,* redescribed recently (Ogden, 1980*b*) from England are listed in Table 1 for comparison. It would appear that the information given does not help to resolve specific identification, which still depends on the measurement of overall body length and differences in shell structure. The significance of these latter features must await morphological studies on clonal cultures.

D. schurmanni is considered to be distinct from *D. gramen* in being smaller, more elongate, having a smooth surface composed of flattish particles and a more open aperture.

Difflugia smilion Gauthier-Lièvre & Thomas, 1958

DESCRIPTION. Unfortunately the only specimen was broken during preparation. The shell is transparent, elongate with a distinct aboral conical protuberance. It is composed mainly of medium to large, angular or flat pieces of quartz to give a rough surface. Organic cement is seen at the junctions of these particles as enclosed spheres, or spheres with small openings, or as a thick rimmed circle with four equal openings (Fig. 12b & c). The spheres are about 600 nm in diameter, the walls of the circle are about 150 nm thick and the internal openings vary between 150–220 nm. The aperture is circular and surrounded mainly by medium sized particles (Fig. 12a).

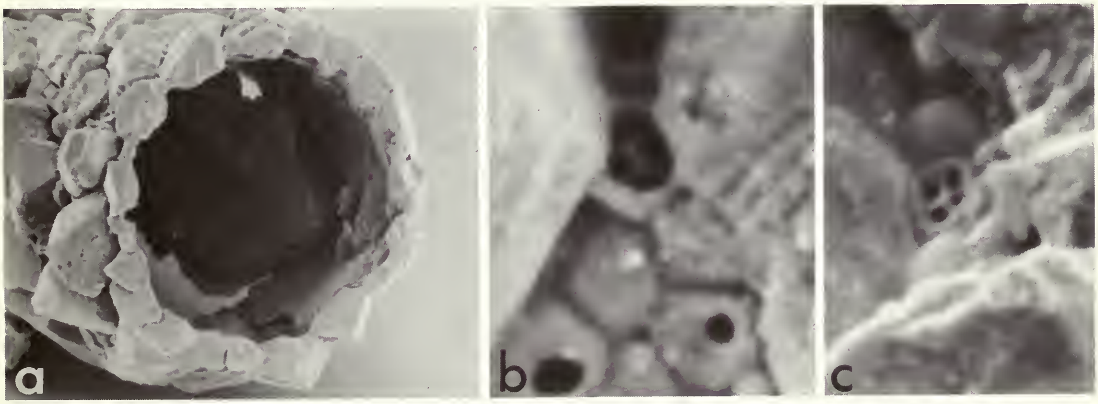

Fig. 12 *Difflugia smilion*: a, apertural view to show arrangement of surrounding particles; b & c, detail of organic cement pattern ×21000 & ×13000.

Table 2 Range of measurements (in μm) of *D. tuberculata* and *D. wailesi*

	n		Length (L)	Breadth (B)	Diameter of aperture (da)	B/L	da/L	da/B
D. wailesi (i)	20	(Y)	84–111	63–103	27–40	0·85±0·09	0·32±0·03	0·38±0·01
D. wailesi (ii)	19	(Y)	73–103	62–82	22–28	0·83±0·07	0·30±0·03	0·36±0·02
D. wailesi	6	(E)	96–112	79–90	29–34	0·80±0·03	0·30±0·01	0·38±0·02
D. tuberculata	6	(Y)	96–116	74–94	31–35	0·82±0·05	0·31±0·02	0·37±0·03
D. tuberculata	27	(E)	102–152	88–141	29–44	0·89±0·10	0·29±0·04	0·33±0·02

n = number of specimens; (i) = typical specimens with indented aperture; (ii) = specimens with circular aperture; E = Norfolk, England (see Ogden, 1980*b*); Y = Yugoslavia (present work)

GEOGRAPHCAL DISTRIBUTION. Algeria (Gauthier-Lièvre & Thomas, 1958), Argentina (Dioni, 1970), Belgium (Chardez, 1980; Chardez & Gaspar, 1976), Brazil (Green, 1975), Congo (Chardez, 1964), France (Thomas, 1953, 1954), Ivory Coast (Gauthier-Lièvre & Thomas, 1958), Poland (Moraczewski, 1965), Roumania (Godeanu *et al.*, 1973).

REMARKS. This specimen is similar in all respects to the description given by Thomas (1953), the body length being about the same, 226 µm, although here it is an estimated figure because of the state of the specimen. No value is given for the breadth, but it was seen to be only slightly larger than the aperture which has a diameter of 41 µm.

Difflugia tuberculata (Wallich, 1864)

Specimens with the typical protuberances were examined and the measurements are included in Table 2.

Difflugia wailesi Ogden, 1980

Difflugia tuberculata var. *minor* Wailes, 1919

DESCRIPTION. Two distinct forms of this species are present in the examined material, both are figured and described.

In the typical form the shell is transparent, ovoid but tapering slightly near the aperture (Fig. 13a). It is composed mainly of flattish pieces of quartz and siliceous elements arranged to give a smooth surface (Fig. 13a). The aperture is polygonal with usually five but occasionally six indentations and bordered by a small lip (Fig. 13b). A ring of about ten small pores is often seen just posterior to the apertural rim.

In the other form the shell is ovoid but more markedly tapered towards the aperture (Fig. 13c). The aperture is circular with no indentations (Fig. 13d), but with a similar small ridge as in the typical form. There are nine or more small tooth-like projections inside the apertural rim on a level with the main body of the shell (Fig. 13e), these tooth-like structures are similar to those sometimes seen at the apex of each apertural projection in the polygonal aperture specimens.

MEASUREMENTS (in µm). See Table 2.

REMARKS. The similarity of dimensions between the present specimens and those reported recently from Norfolk, England, highlight the difficulty of differentiating the two species *D. tuberculata* and *D. wailesi*. A further division of *D. wailesi* is not desirable unless supported by strong morphological evidence, therefore, although the specimens are reported as two groups no particular significance is attached to these differences.

Difflugia balcanica sp. nov.

DESCRIPTION. The shell is transparent, ovoid or roughly circular with an aboral cone or spine and laterally compressed, the shape resembles either an arrow-head or a leaf (Figs 14a & c). It is composed of a mixture of small to large pieces of mainly flattish quartz, arranged to give a relatively smooth but irregular surface, unfortunately the illustrated specimen has some overlying debris scattered on the anterior third of the body. An open network of organic cement is seen between the particles. The aperture is roughly circular and surrounded by small or medium pieces of quartz (Fig. 14b).

MEASUREMENTS (in µm). Two specimens: body length 111–114, breadth 79–82, depth 50, diameter of aperture 31.

REMARKS. There does not appear to be any prior descriptions of any similar compressed species of *Difflugia*, and *D. balcanica* is considered to be distinct in having a leaf-like shape, with an angular surface and a pointed aboral extremity.

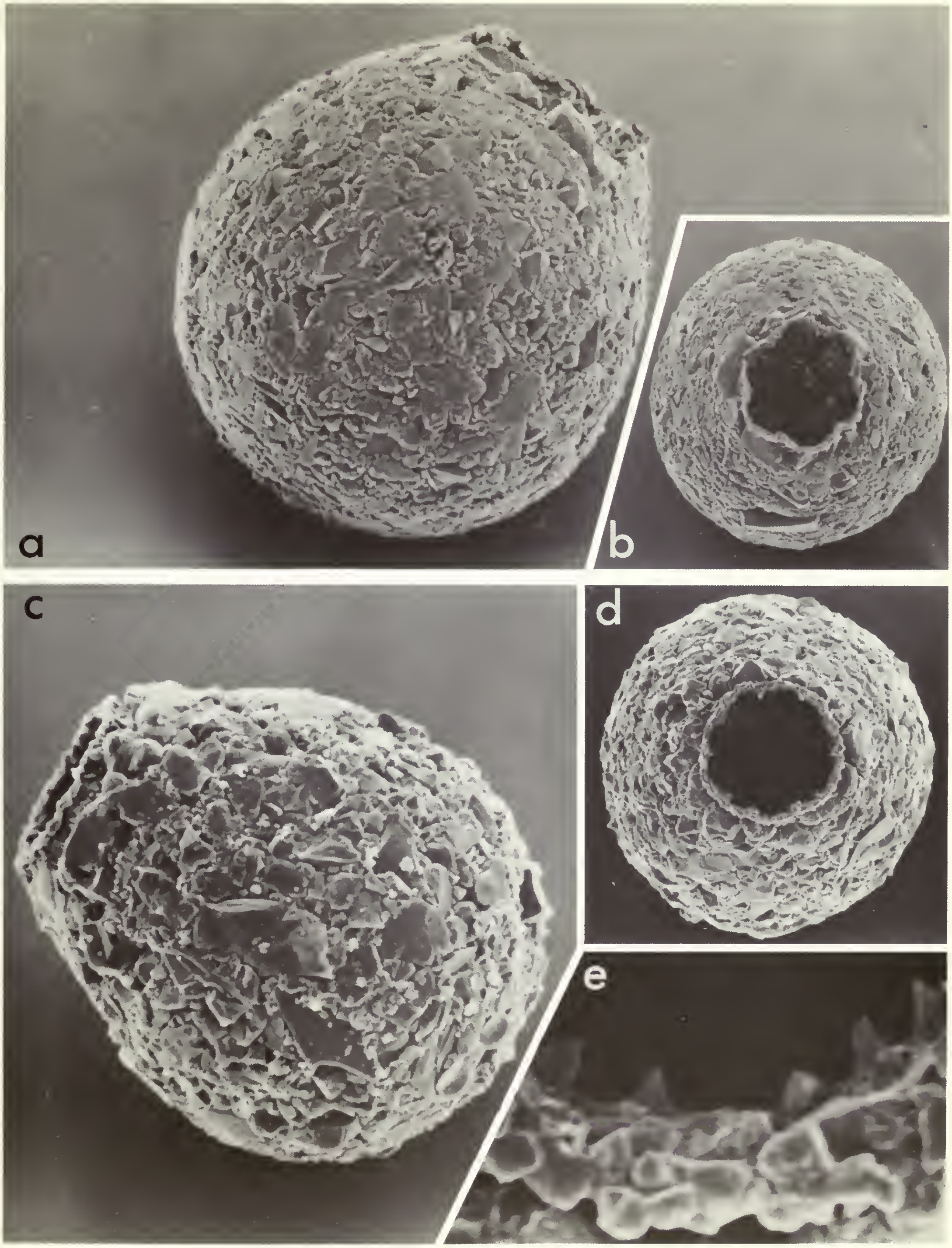

Fig. 13 *Difflugia wailesi*: a, lateral view of typical specimen ×760; b, apertural view of a, note the six indentations ×470; c, lateral view of elongate specimen ×1100; d, apertural view of; c, to show circular aperture and surrounding collar ×720; e, detail of teeth on inner rim of circular aperture ×5100.

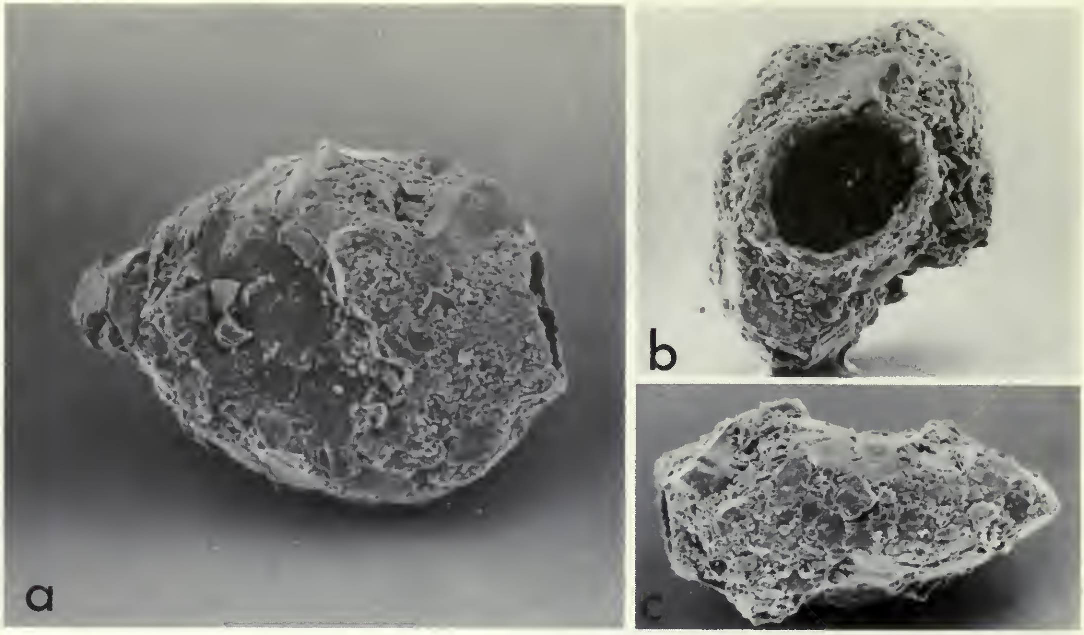

Fig. 14 *Difflugia balcanica* sp. nov.: a, view to illustrate general outline with aboral protuberance ×570; b, apertural view ×620; c, lateral view to show compression, note the tapering at the apertural and aboral extremities ×460.

Difflugia bistrica sp. nov.

Description. The shell is ovoid or roughly circular, thin and laterally compressed (Fig. 15a & b). It is composed of medium flattened pieces of quartz with smaller particles between to give a smooth surface (Fig. 15d). Small areas of organic cement occur infrequently, and are usually in the form of a network (Fig. 15e). The aperture is a regular oval and surrounded by small particles (Fig. 15c).

Measurements (in µm). One specimen: body length 104, breadth 84, depth 54, diameter of aperture 38.

Remarks. Although this specimen has an encrustation of small debris, which is not part of the shell matrix (see Fig. 15d), it is still possible to describe the surface as smooth. This species is similar to *D. balcanica* in dimensions and degree of compression, but differs significantly in having a rounded, smooth shell which is curved gently at the aboral extremity. Notwithstanding that this description is based on a single specimen, it is still considered to represent a distinct species and is so designated.

Difflugia dragana sp. nov.

Description. The shell is opaque, elongate ovoid, thick, tapering gradually from the mid-body position to a gracefully curved aboral extremity and anteriorly to the suggestion of a small apertural collar, it is laterally compressed (Figs 16a & b). Medium pieces of quartz appear to make up most of the surface with smaller particles added. Only small strands of organic cement have been seen (Fig. 16d) between these particles. The aperture is circular and surrounded by mainly small particles of quartz (Fig. 16c).

Measurements (in µm). One specimen: body length 195, breadth 119, depth 96, diameter of aperture 48.

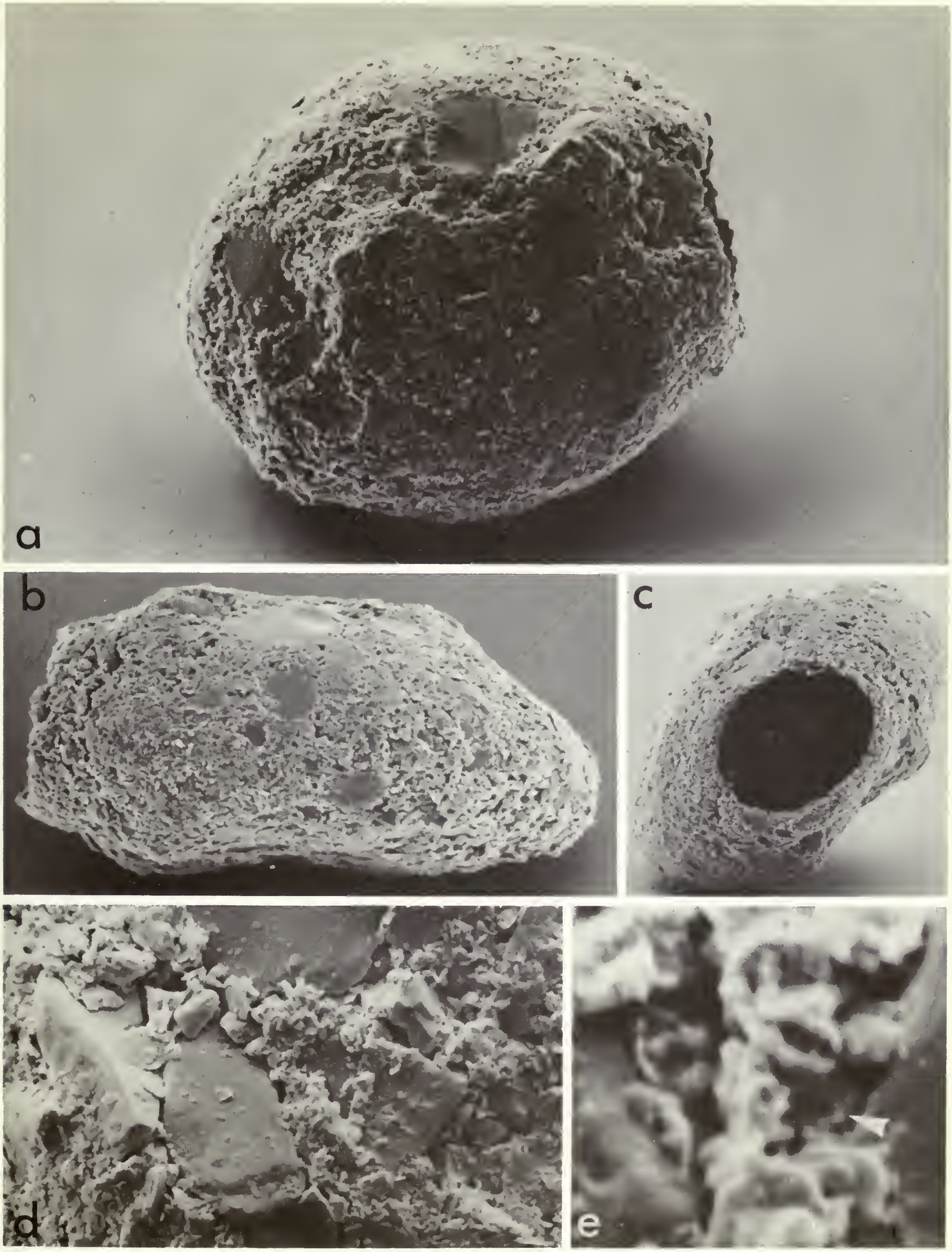

Fig. 15 *Difflugia bistrica* sp. nov.: a, lateral view to show regular, circular shape × 760; b, view to illustrate lateral compression, note the gentle aboral curvature × 720; c, apertural view showing oval-shaped aperture × 660; d, portion of shell surface to show flat particles overlaid with extraneous debris × 2900; e, organic cement (arrowed) partially obscured by debris × 13000.

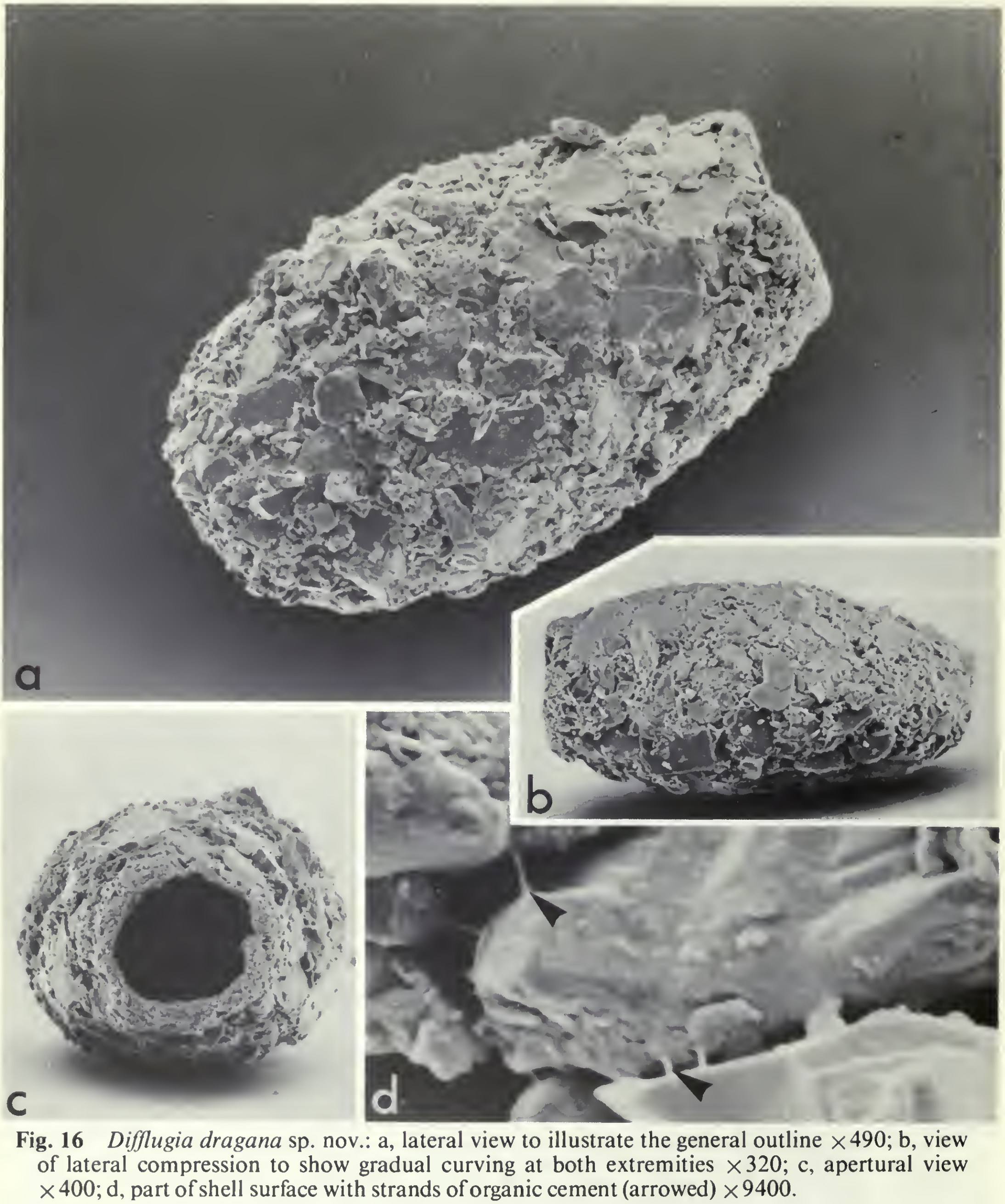

Fig. 16 *Difflugia dragana* sp. nov.: a, lateral view to illustrate the general outline ×490; b, view of lateral compression to show gradual curving at both extremities ×320; c, apertural view ×400; d, part of shell surface with strands of organic cement (arrowed) ×9400.

REMARKS. This compressed specimen is similar to *D. lingula* Penard, 1911, *D. avellana* Penard, 1890 and *D. hiraethogii* Ogden, 1983. It differs from *D. lingula* and D. *avellana* which have pyriform shells, because of the narrow, elongate body which is almost cigar-shaped in lateral view (Fig. 16b), and wide aperture. Although it is most similar to *D. hiraethogii,* it lacks the distinct neck of this species and is again more elongate and not evenly compressed. *D. dragana* is considered to be distinct in having an elongate, compressed shell with a wide aperture.

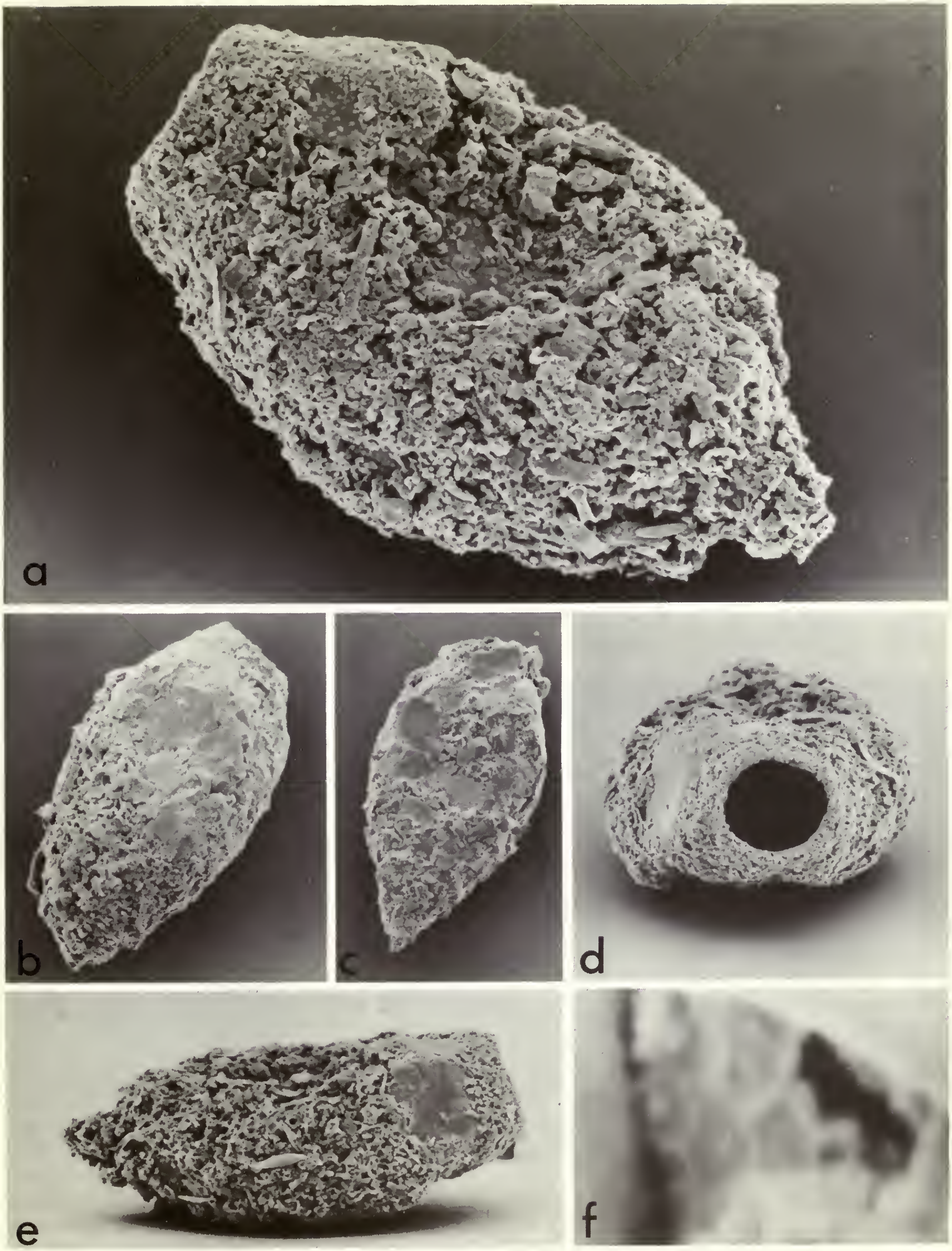

Fig. 17 *Difflugia serbica* sp. nov.: a, lateral view of specimen encrusted with extraneous debris ×680; b & c, additional specimens to illustrate the variations of tapering ×310 & 240; d, apertural view ×420; e, view to show lateral compression ×400; f, detail of organic cement network ×21000.

Etymololgy. This species is named after Dragana Dorothea Živković, who has been most helpful in correcting the language shortcomings of both authors.

Difflugia serbica sp. nov.

Description. The shell is opaque, shaped like a spear-head, tapering evenly from the body to the pointed aboral extremity and gradually, anteriorly towards the short apertural collar, it is laterally compressed (Figs 17a–e). The body is composed mainly of medium to large flattish pieces of quartz with a mixture of small to medium pieces at the aperture and aboral extremity. Although the surface is usually smooth, two of the specimens are covered with a layer of small particular debris which appears to have been added after the shell was constructed (Fig. 17e). The organic cement is not frequently seen but is in the form of a network, the mesh being about 400 nm in diameter with walls 50 nm thick, each mesh being covered (Fig. 17f). The aperture is circular and usually surrounded by small particles (Fig. 17d).

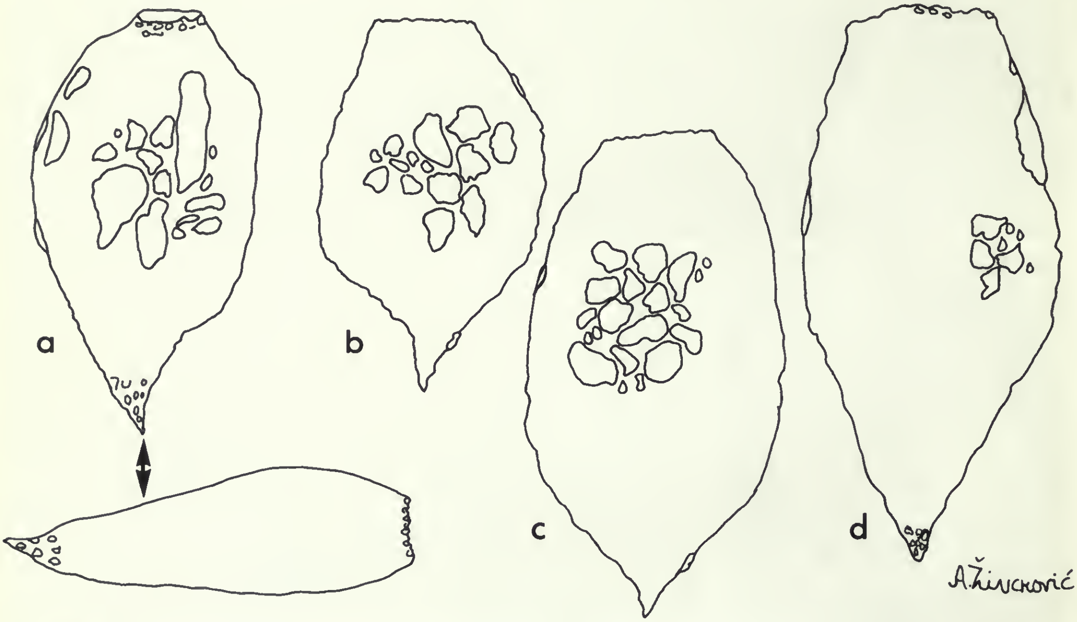

Fig. 18 *Difflugia serbica* sp. nov. Diagrams of four specimens to show the variation in outline.

Measurements (in µm). Five specimens: body length 169–189, breadth 110–113, depth 68–79, diameter of aperture 31–41.

Remarks. The dimensions of five specimens from the Yugoslavian sample were somewhat larger: body length 180–280, breadth 110–160, depth 75–115 (only two measured), diameter of aperture 40–70. Nevertheless, they demonstrate a similar variability in general shape and structure (Fig. 18). This species is similar to *D. soudanensis* Gauthier-Lièvre & Thomas (1958) and *D. kempyi* Stěpánek, 1953 in general dimensions, but both of these species have a distinct apertural collar, are curved aborally and have a median pronounced spine or horn. Furthermore, of these two species only *D. soudanensis* is compressed. *Difflugia serbica* is considered to be distinct in having an irregular spear-shaped shell which is laterally compressed, with the suggestion of a small apertural collar and usually pointed aborally.

Difflugia serrata sp. nov.

Description. The shell is transparent, ovoid, composed of small to medium flattish particles

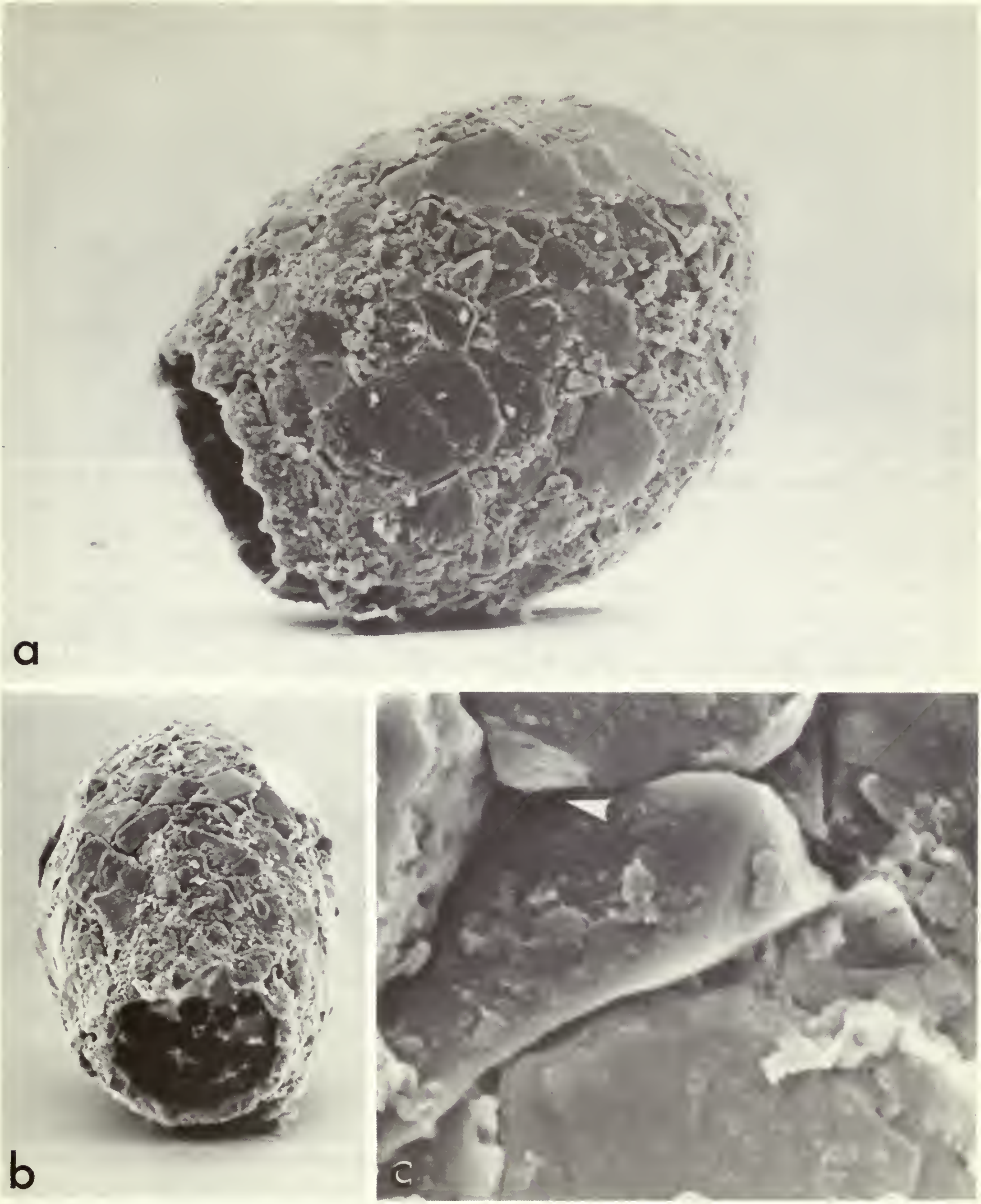

Fig. 19 *Difflugia serrata* sp. nov.: a, lateral view, note the serrated apertural margin ×1300; b, apertural view ×930; c, portion of shell surface with organic cement (arrowed) ×9400.

of quartz arranged to give a smooth surface (Fig. 19a). Organic cement is seen as small strands or as a smooth sheet, with regular perforations about 50 nm in diameter (Fig. 19c). The aperture is circular with a slight irregular or serrated margin (Figs 19a & b).

Measurements (in µm). One specimen: body length 66, breadth 56, diameter of aperture 28.

Remarks. This species is distinct from other ovoid species of similar dimensions, like *D.*

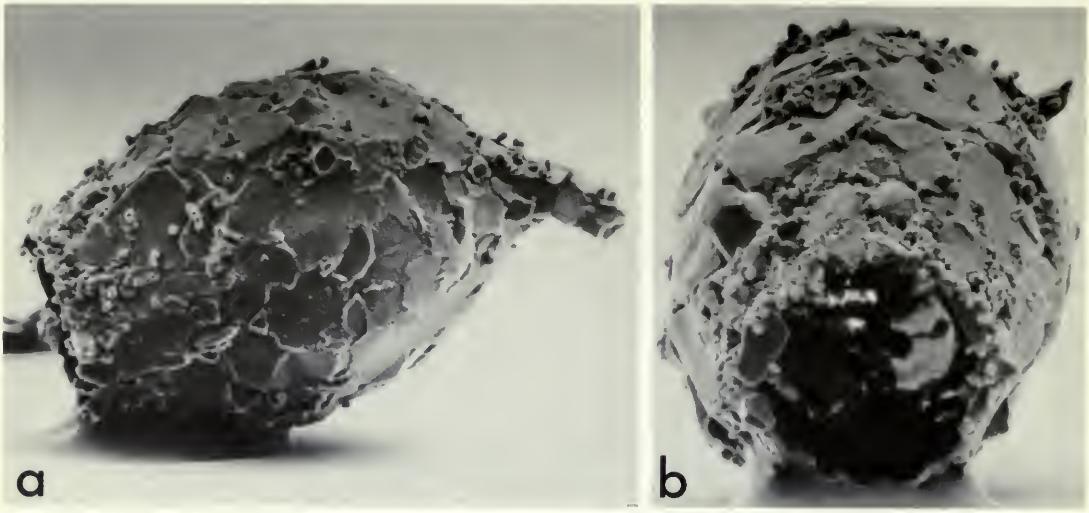

Fig. 20 *Difflugia styla* sp. nov.: a, lateral view to illustrate the aboral spine and smooth surface ×700; b, apertural view ×960.

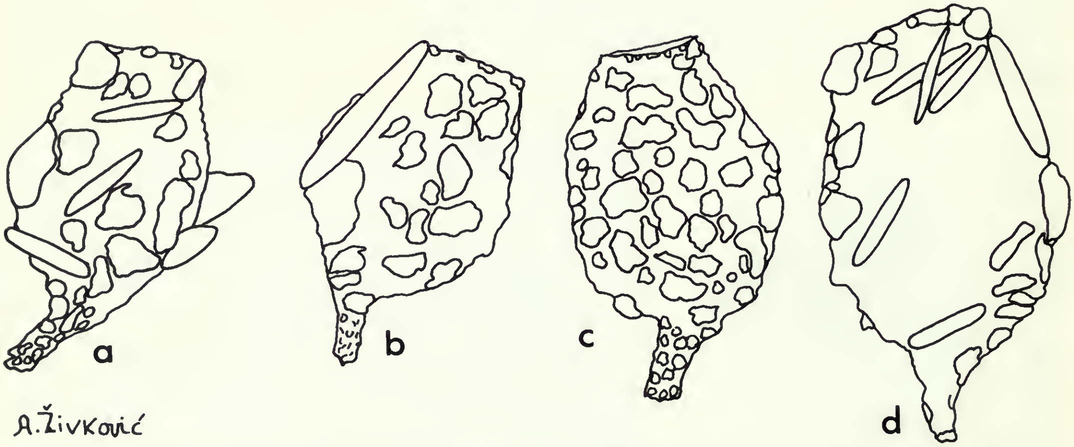

Fig. 21 *Difflugia elegans.* Illustrations of four specimens, the typical constriction of the neck can be seen in a.

minuta Rampi, 1950 and *D. pristis* Penard, 1902 which have recently been redescribed by Ogden (1983), in having a thin smooth shell and a wide aperture. It is most similar to *D. pristis,* but the more ovoid or rounded shell, with a large and serrated aperture serve to distinguish *D. serrata.*

Difflugia styla sp. nov.

DESCRIPTION. The shell is transparent, ovoid with a distinct aboral spine (Fig. 20a). It is composed of small to medium flattish pieces of quartz, and a network of organic cement is often seen around the aperture as part of the shell matrix. Elsewhere on the surface the organic cement is seen as strands between particles. The aperture is circular and surrounded by smallish particles (Fig. 20b).

Measurements (in µm). One specimen: body length 97, breadth 54, diameter of aperture 29.

Remarks. This species is similar to *D. elegans* or *D. bicornis* (see p. 000) in having a single aboral spine or horn. However, both of these latter species are described as having a rough, irregular surface made of angular quartz particles and diatom frustules. In addition, *D. elegans* has a slight constriction of the neck which gives the aperture a flared appearance (Ogden, 1979), and it was found in the Yugoslavian portion of the sample to show these features (Fig. 21). Although *D. styla* shares similar dimensions to *D. serrata* (see p. 000) the presence of an aboral spine separates these species. *D. styla* is distinct in being elongate ovoid with an aboral spine, and having a smooth shell composed of flat particles.

Genus ***CUCURBITELLA*** Penard, 1902

Cucurbitella vlasinensis sp. nov.

Description. The shell is brown or opaque, subcircular or ovoid, with a distinct apertural collar (Fig. 22a). It is composed of a mixture of small to medium pieces of quartz to give a rough surface, but arranged so that the outline is more or less regular. The particles are packed close together (Fig. 22f), with only small areas of organic cement visible. The cement is in the form of a network whose mesh is covered by a smooth membrane (Fig. 22e). The collar is trilobed and composed of small pieces of quartz arranged randomly (Fig. 22b). A double thickness of particles strengthens the three tooth-like projections where they form a dividing barrier with the inner apertural opening; these 'teeth' are usually well defined and composed of small particles. Each lobe has a small recess or cavity so that the internal opening is smaller than the external collar, the floor of these recesses appears as a continuation of the shell matrix (Fig. 22d). The apertural opening is trilobed in sequence with the collar and lined with flattish pieces of quartz with smaller pieces filling the junctions (Fig. 22c).

Measurements (in µm). Forty-one specimens: body length 81–113, breadth 69–97, diameter of collar 36–51, depth of collar 9–16, diameter of aperture 19–35.

Remarks. In a review of the genus *Cucurbitella* by Gauthier-Lièvre & Thomas (1960) the number of lobes surrounding the aperture was used to differentiate species into a number of varieties and forms. More recently, Ogden (1980*b*) considered that the three and four lobed specimens of *C. mespiliformis* were otherwise identical in all but that feature, and should therefore be designated as a single species until adequate morphological information was available on the variability of lobe formation. Nevertheless, observations on the many specimens of the present sample show that there is little or no variation in the number and shape of the lobes. *C. vlasinensis* is similar to *C. modesta* Gauthier-Lièvre & Thomas, 1960 and *C. modesta* forma *trilobata* Gauthier-Lièvre & Thomas, 1960. It differs from *C. modesta,* which has four lobes, in that feature and general measurements, and from *C. modesta* forma *trilobata* in having well-defined teeth, a more extensive inner lining to each lobe and in overall larger general dimensions.

An interesting ecological point to note is that *C. modesta* forma *trilobata* was reported only from Morocco which has similar climatic conditions to the region of Yugoslavia where the present samples were collected.

Etymology. This species is named after the location where the samples were collected, Lake Vlasina, and which, after a visit by both authors in 1982, has become especially significant.

Genus ***PONTIGULASIA*** Rhumbler, 1895

Pontigulasia bryophila Penard, 1902

Description. The shell is pyriform, tapering from the aperture to the slightly swollen posterior third of the body (Fig. 23a). It has a rough surface composed of a mixture of quartz particles with an occasional diatom frustule added. Organic cement is seen at the junctions

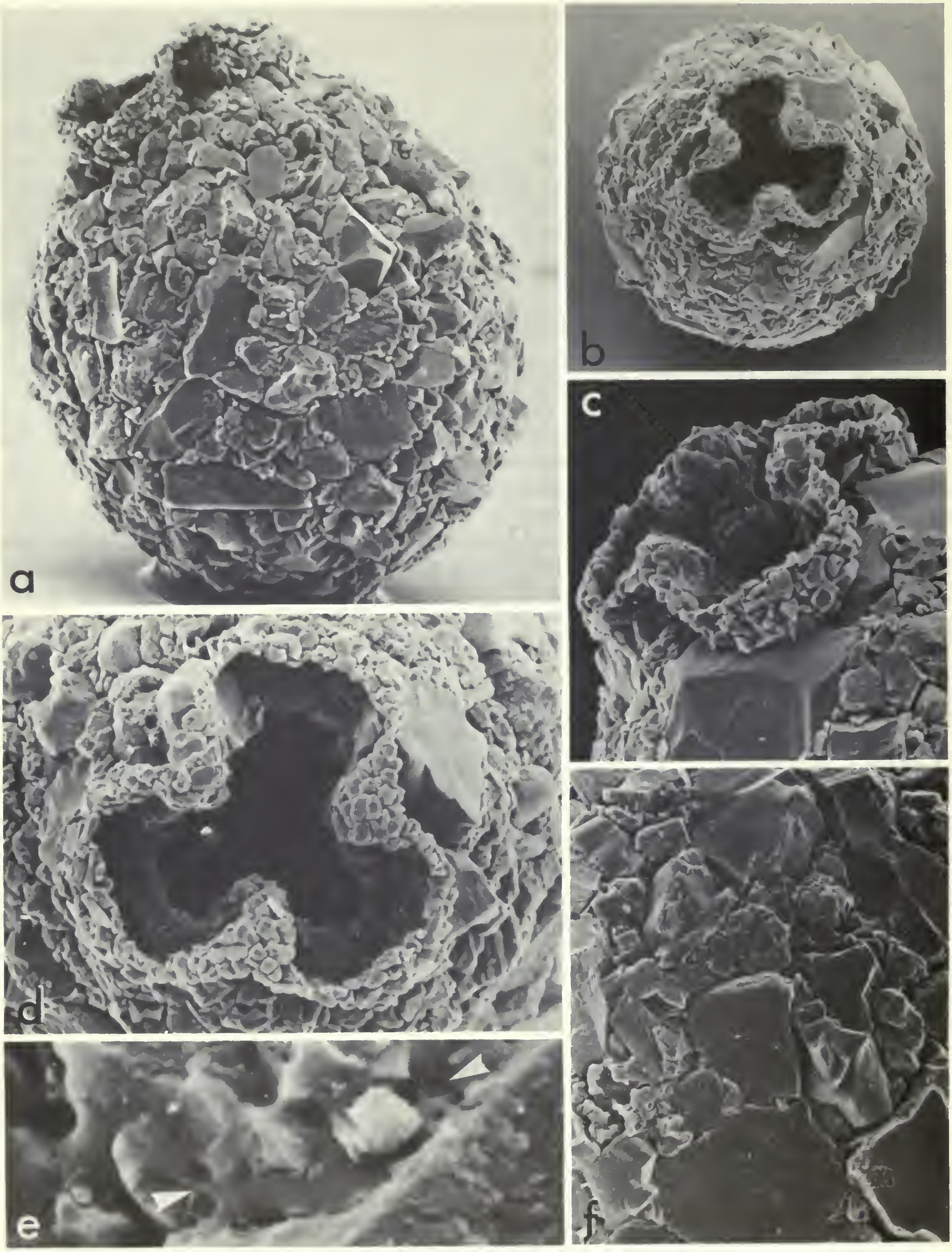

Fig. 22 *Cucurbitella vlasinensis* sp. nov.: a, lateral view × 830; b, apertural view × 540; c, view to illustrate the arrangement of particles around the collar × 1200; d, detail of aperture to show tooth-like projections and smaller internal opening × 1200; e, detail of organic cement (arrowed) × 13000; f, portion of shell surface showing the close packing of particles × 1500.

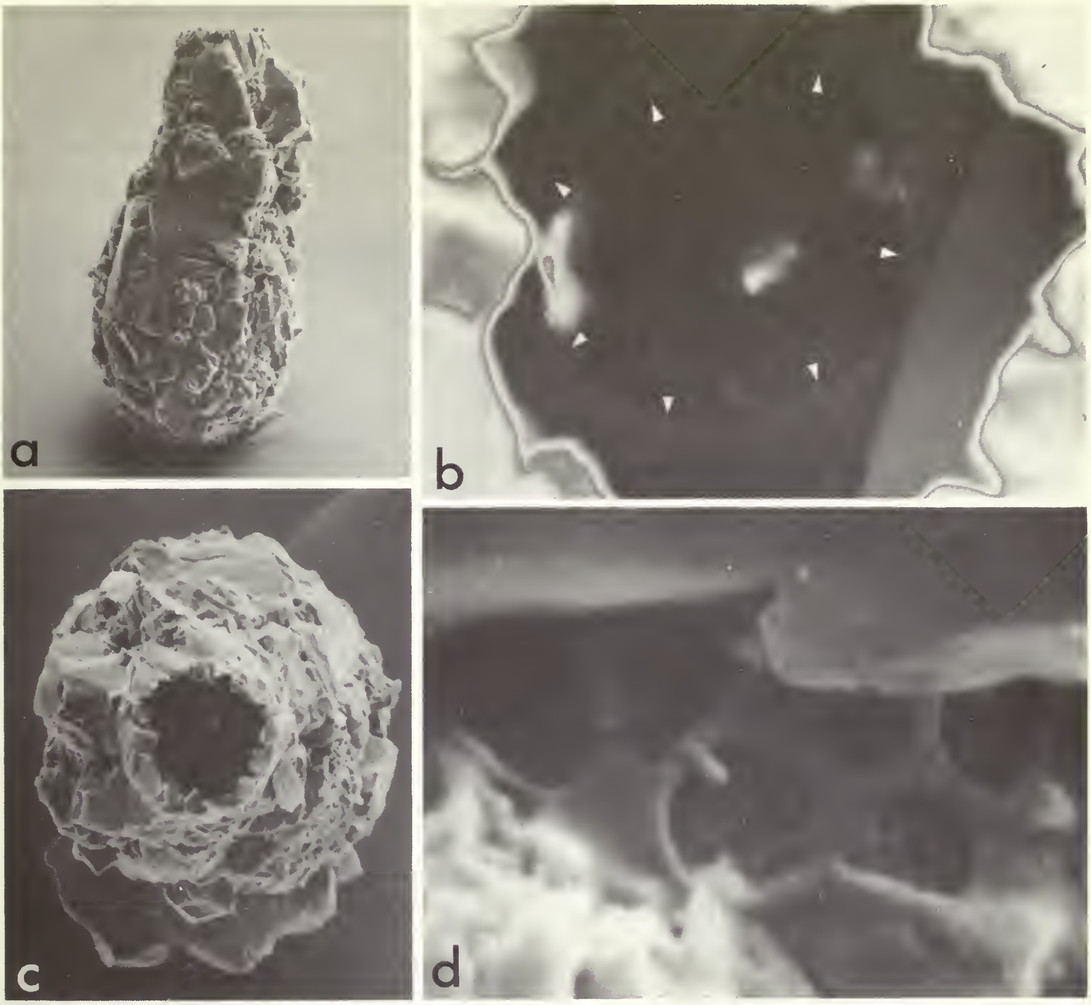

Fig. 23 *Pontigulasia bryophila*: a, lateral view ×470; b, view inside external aperture to show the internal aperture opening (arrowed), micrograph obtained by 'expanded contrast' facility ×4100; c, apertural view ×760; d, detail of organic cement to illustrate the smaller irregular network of each mesh enclosure ×29000.

between particles as a network. This network has a mesh about 600 nm in diameter separated by walls 200 nm thick. Each enclosure has a smaller irregular network over its surface (Fig. 23d). The external aperture is small, surrounded by small or medium particles often arranged to give a serrated or tooth-like margin (Fig. 23c). The single, internal aperture is roughly circular (Fig. 23b) and positioned about a quarter of the body length from the external aperture.

Measurements (in µm). See Table 2.

Remarks. This species is similar in general appearance to *Difflugia bryophila* but may be distinguished from it by the presence of an internal aperture and a different organic cement pattern. The present specimens are similar in most respects to specimens of *P. bryophila* found in England (C.G.O. pers. observ.) except for a difference in organic cement patterns. This feature alone is not considered sufficient for specific recognition.

Pontigulasia montana sp. nov.

DESCRIPTION. The shell is pyriform, bluntly rounded aborally for one-third of its length and usually tapering gradually from the widest point towards the aperture (Fig. 24a), although sometimes there is a distinct constriction at the position of the internal aperture (Fig. 24c). It is composed of a mixture of mainly medium to large pieces of quartz arranged to give a rough surface. Organic cement is often seen as part of the shell matrix (Fig. 24d), in the form of an

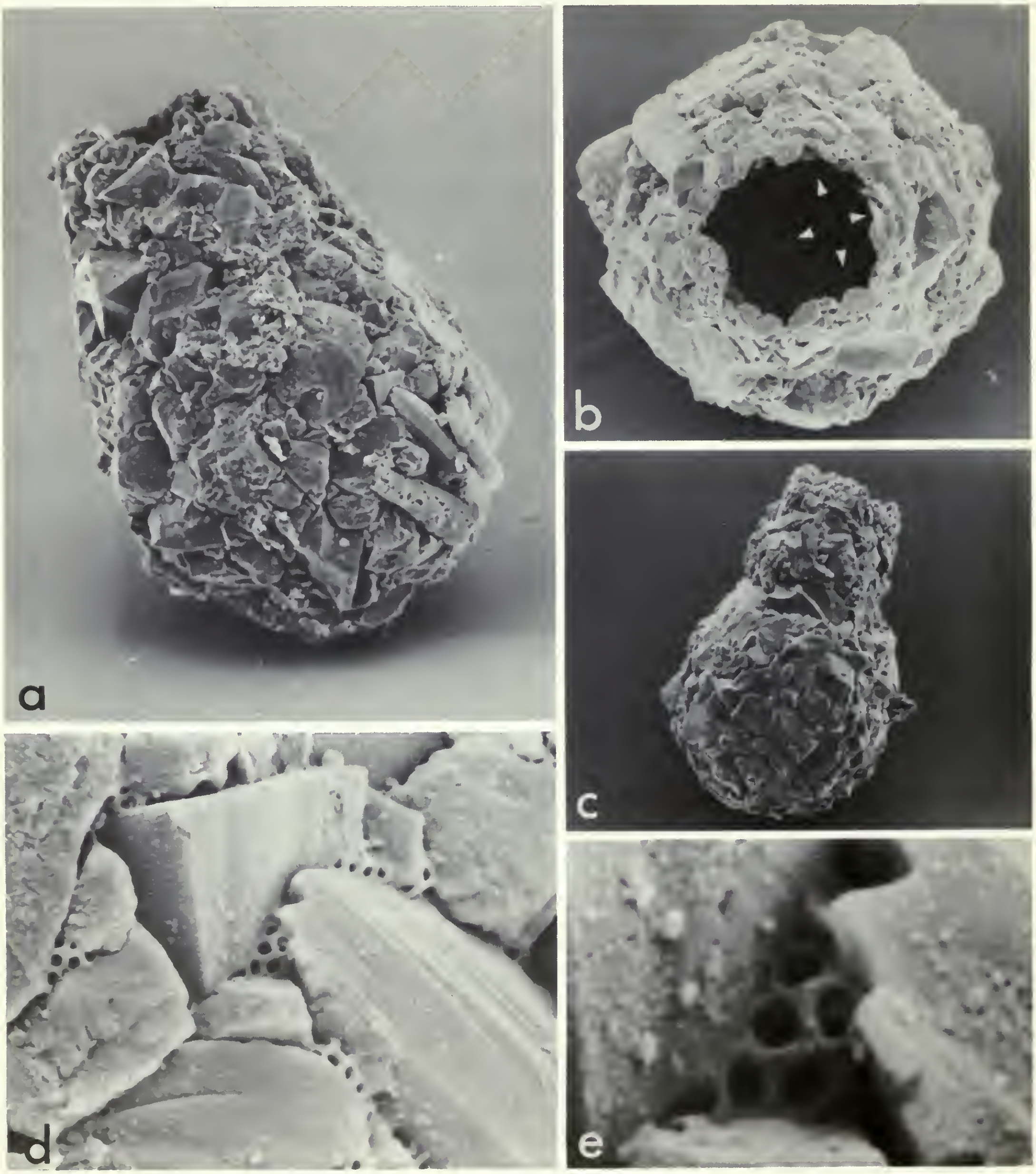

Fig. 24 *Pontigulasia montana* sp. nov.: a, lateral view of specimen without neck constriction ×730; b, apertural view with the internal aperture arrowed ×730; c, lateral view of specimen with distinct neck constriction ×430; d, portion of shell surface showing organic cement as part of the shell matrix ×4400; e, detail of organic cement network ×14000.

open network with walls 200 nm thick and a mesh diameter of 400 nm (Fig. 24e). The external aperture is roughly circular and surrounded by small or medium particles randomly positioned to give it an irregular margin (Fig. 24b). The smaller, single, internal aperture is also circular and surrounded by small particles overlaid with organic cement.

Measurements (in µm). See Table 3.

Table 3 Range of measurements (in µm) of two species of *Pontigulasia*

	n	Length (l)	Breadth (B)	Diameter of external aperture (da)	Diameter of internal aperture	B/L	da/L
P. bryophila	4	99–146	52–66	18–21	11–14	0·52±0·05	0·15±0·03
P. montana	5	91–125	68–81	28–32	15–18	0·69±0·07	0·28±0·03

Remarks. The specimens described here are similar to *Pontigulasia bryophila* Penard, 1902, but the latter species has a more streamlined, elongate shell, with smaller internal and external openings, plus a distinct organic cement pattern. Comparison of the measurements given in Table 3 emphasizes the difference in body and apertural size between these two species, furthermore, *P. bryophila* appears to be the only previously described species of *Pontigulasia* with a single internal aperture.

Etymology. This species is named after the geographical topography surrounding Lake Vlasina, which is mountainous (*L. montana*).

Summary

The information provided by this study extends our knowledge of the family Difflugiidae, in particular the finding of compressed species of *Difflugia*. The scarcity of these forms is perhaps highlighted by the review of African species in which Gauthier-Lièvre & Thomas (1958) list twelve compressed species, of these nine were new, out of a total of one hundred and thirty-three. Thirty-three species of *Difflugia* are listed here of which thirteen are re-described, including two former varieties of *D. oblonga* — namely *D. lata* and *D. nodosa,* six new species are described — *D. balcanica, D. bistrica, D. dragana, D. serbica, D. serrata* and *D. styla* the first four having compressed shells. In addition, two other new species are described — *Cucurbitella vlasinensis* sp. nov. and *Pontigulasia montana* sp. nov.

It has been mentioned before (Ogden, 1980*b*) that the size and shape of the aperture in pyriform species of *Difflugia* is a relatively uniform character, but in ovoid specimens appears more variable as shown here in the description of *D. lismorensis.*

Morfološka studija nekih Difflugiidae iz Jugoslavije (Rhizopoda, Protozoa)

REZIME

Podatke date u ovom radu proširuju naša znanja o familiji Difflugiidae, naročito u pogledu otkrivanja pljosnatih vrsta *Difflugia*. Retkost ovih vrsta možda se najbolje ogleda u radu o afričkim vrstama, Gauthier-Lievre i Thomas (1958), u kome je dat spisak od ukupno 133 vrsta; medju njima je dvanaest pljosnatih vrsta, od kojih je devet novih. Ovaj rad sadrži spisak od tridesettri vrste *Difflugia*, od kojih su trinaest ponovo opisane, uključujući i dva ranija varijeteta: *D. oblonga*, odnosno *D. lata* i *D. nodosa*, a opisano je i šest novih vrsta — *D. balcanica, D. bistrica, D. dragana, D. serbica, D. serrata* i *D. styla,* od kojih prve

četiri poseduju pljosnate ljušture. Opisane su i dve nove vrste — *Cucurbitella vlasinensis* sp. nov. i *Pontigulasia montana* sp. nov.

U ranijim publikacijama ukazano je (Ogden, 1980*b*) da su veličina i oblik pseudostoma u piriformnim vrstama *Difflugia* relativno konstantna, medjutim, pojavljuje se veća varijabilnost u ovoidnim uzorcima, kao što je slučaj u *D. lismorensis*.

Proučeni materijal sakupljen je 9 septembra 1947. godine iz jedne bare sa prostrane sfagnumske tresave na Vlasini (1200 m) koja je izgradnjom akumulacionog jezera izčezla.

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British Museum (Natural History)

An Atlas of Freshwater Testate Amoebae

C. G. Ogden & R. H. Hedley

1980, Hardcovers, 222pp, £17.50 (£18.00 by post). Co-published by British Museum (Natural History) and Oxford University Press.

This book illustrates, using scanning electron micrographs, most of the common species of testate amoebae that are found in freshwater habitats. Information on the biology, ecology, geographical distribution and a classification are followed by descriptions of ninety-five species. Each of these is illustrated by several views of the shell.

The text is designed not only to enable biologists to identify species of testate amoebae, but to serve as an introduction to students interested in the taxonomy and biology of these freshwater protozoa. It will be of special interest to protozoologists, ecologists, limnologists, water treatment specialists and micropalaeontologists interested in recent sediments.

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